AN ABSTRACT OF THE THESIS OF

Roberto C. Meléndez for the degree of Doctor of Philosophy in Fisheries Sciences presented on April 17, 1995. Title: Phylogeny and Zoogeography of Laemonema (Pisces; Gadiformes; Moridae).

Redacted for Privacy

Abstract approved: ___________________

Douglas F. Markle

The systematics of the "*Laemonema*" subgroup plus *Paralaemonema*, was conducted based on 480 juvenile and adult specimens from around the world. A cladistic analysis supported recognition of two genera, *Laemonema* with 12 species, and *Guttigadus* with eight species, including two of uncertain status.

Two new species of *Laemonema* are described from the Indian Ocean and western Atlantic. Juvenile stages, previously assigned to *Svetovidovia* Cohen, are described for *L. barbatulum*, *L. melanurum* and the new western Atlantic form. These juveniles have as many as eleven pelvic fin rays, whereas adults have only two, indicating ontogenetic resorption of inner pelvic fins rays.

Momonatira Paulin and *Paralaemonema* Trunov are considered junior synonym of *Guttigadus*. Four species previously assigned to *Laemonema*, are reassigned to *Guttigadus*, *G. globiceps*, *G. latifrons*, *G. kongi*, and *G.*

nana. One species, G. nana, representing the earliest clade in Guttigadus is a dwarfed, pelagic, paedomorphic species. The known juveniles stages of Guttigadus have numerous vertical bars on body not found in Laemonema.

Laemonema and Guttigadus are largely allopatric. Laemonema is primarily in tropical waters between 60° N and 40° S, being more abundant at approximately 200-600 m depth, and absent in the northeastern Pacific and eastern Indian Ocean. Four terminal species pairs of Laemonema are allopatric, each showing east-west segregation. One Atlantic pair may also show depth segregation, with L. barbatulum found to depths of 1620 m and L. yarrelli to 550 m. Guttigadus is primarily in the Southern Ocean, between 25° and 59° S, and is most abundant at approximately 600-1600 m depth. Two species of Guttigadus range into the Northern Hemisphere, G. nana in the western North Pacific and G. latifrons in the eastern North Atlantic. Segregation of the sympatric sister taxa, G. kongi and G. globosus, may have been partly bathymetric, the former most abundant at 500-800 m and the latter living at 1175-1600 m.

Phylogeny and Zoogeography of Laemonema (Pisces; Gadiformes; Moridae)

by

Roberto C. Meléndez

A THESIS

submitted to

Oregon State University

in partial fulfillment of

the requirement for the

degree of

Doctor of Philosophy

Completed April 17,1995

Commencement June 1996

Doctor of Philosophy thesis of Roberto C. Meléndez presented

on April 17, 1995

APPROVED:

Redacted for Privacy

Major Professor, representing Fisheries Science

Redacted for Privacy

Head of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Redacted for Privacy

Roberto C. Meléndez, Author

To my wife María Angélica
and my sons María Constanza,
Roberto Andrés and Juan Pablo.

To my Father, brothers and
sisters.

In the loving memory of my
Mother.

ACKNOWLEDGMENTS

I would like to thank my major professor Dr. Douglas F. Markle, who gave me the opportunity to begin a new step in my life back in September 1987, thank you very much for your infinite patience while review the drafts, also for encouragement, support, friendship, and hospitality.

To the members of my committee Drs. Arthur J. Boucout, William J. Liss, Tomio Iwamoto and Evelyn Sherr, and former members Daniel M. Cohen, B. J. Verts and Frank Conte. Special acknowledgments to Dr. Daniel M. Cohen for his invaluable help with his experience and the sharing of all his knowledge in gadiform fishes, as well as his hospitality when I was at Los Angeles, California.

I would like to thank to Oregon State University Sea Grant who support me during my first year at the Department of Fisheries and Wildlife through program MA85AA-D-5G-095, E/ISG6 (1987-1988), and support a trip to Smithsonian Institution, Washington D.C. and to Los Angeles County Museum of Natural History, Los Angeles, California. The Organization of American States (OAS) through the scholarship F 04501 (1988-1990). The Agencia de Cooperación Internacional (AGCI) from the Ministerio de Planificación y Cooperación, Chile, which support me to come back to Oregon State University to defend the present thesis (1994-1995). Finally, the International Committee for Migration helped me with the roundtrip airfare for my wife and children (1988-1990).

To Ing. Hans Niemeyer F. and Prof. Luis Capurro S., former and present Directors of the National Museum of Natural History at Santiago, Chile, and to the present and formers Directors of the Dirección de Bibliotecas, Archivos y Museos de Chile (1987-1995) for their authorization to continue my studies abroad.

Many people from different museums and institutions around the world help me with the loan of fish specimens specially, Kunio Amaoka, Carole C. Baldwin, M. L. Bauchot, Manuel José Biscoito, Ingvar Byrkjedal, George H. Burgess, Daniel M. Cohen, William Eschmeyer, William Fink, Ofer Gon, J. P. Gosse, Lou Van Guelpen, Karsten E. Hartel, P. Alexander Hulley, Susan Jewett, Jeff Johnson, Christine Karrer, Osamu Okamura, Thomas M. Orrell, G.E. Maul, Mark McGrouther, Nigel Merret, Douglas W. Nelson, Jorgen Nielsen, N. V. Parin, Chris Paulin, Y.I. Sazonov, Mathias Stheman, and Alwyne Wheeler.

To my friends and colleagues of the Museo Nacional de Historia Natural, Santiago, Chile, mainly those of Sección Hidrobiología, who helped me in many way during my staying at Oregon State University.

To my former classmate Phil Harris and friends, Gonzalo Castillo, Jorge Mesías, Paulo Petry, Todd Pearsons, Chris Donoghue, and many others to whom I meet at Corvallis, they made my life more easy. Phil helped me with PAUP Unix version and Chris helped me with the use of various software. Special thanks to Dr. David L. Stein, former professor of Oceanography at O.S.U., he also gave me guidance in the knowledge of fishes. To Steve and Irene Neshyba, Richard and Leona Converse and Erika Salinas, thank you for your hospitality.

Finally, to my wife María Angélica, for her love, support, and understanding mainly while we were at Corvallis, and taken care of everything in Chile when I was abroad. Also to my children María Constanza, Roberto Andrés and Juan Pablo, they gave the strength when I was alone, and tender company and love while together in Corvallis.

CONTRIBUTIONS OF AUTHORS

Roberto C. Meléndez, responsible for collecting data, initial analysis, and writing of first draft. Dr.Douglas F. Markle, responsible for error checking, re-writing, and detailed re-analysis.

This thesis will be submitted to the Bulletin of Marine Sciences and it is formatted according with their instructions.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

LIST OF TABLES

LIST OF TABLES (Continued)

PHYLOGENY AND ZOOGEOGRAPHY OF LAEMONEMA (PISCES; GADIFORMES; MORIDAE)

INTRODUCTION

According to Cohen et al. (1990), half of the known species of gadiform fish live in deep water, are mainly small, some are apparently rare, and many have taxonomic problems. Cohen (1989) stated, "... gadiform systematics remains far from a closed book...". Svetovidov (1948), recognized the family Moridae, separate from Gadidae, based on the presence of an entire osseous canal for the olfactory nerves, an interorbital septum that is largely osseous, presence of fontanelles in the back of the neurocranium, and an otophysic connection between the swimbladder and the auditory capsules. Svetovidov (1948) included Mora, Lepidion, Physiculus, Laemonema, in Moridae. Cohen et al. (1990) included 19 genera and 91 species in Moridae but indicated that the list is not complete because of many taxonomic problems.

Karrer (1971) recognized three groups of genera in Moridae, one of them, the Physiculus group (Physiculus, Tripterophycis and Laemonema), is characterized by spindle-shaped otoliths and presence of luminescent organs. However, her groupings are problematic because Laemonema does not have luminescent organs. She noted that Laemonema might be polyphyletic.

Paulin (1983) described several morphological characteristics of morid fishes from New Zealand, although the taxonomic and phylogenetic value of the characters was not well documented. Paulin (1989) divided Moridae into three groups based mainly on the shape of the otoliths. The "*Mora*" group included the genera *Mora*, *Halargyreus*, *Lepidion*, and *Antimora*, with cup-shaped bend on the crista inferior. The "*Pseudophycis*" group included *Pseudophycis*, *Lotella*, and *Eyorius*, with the ostium approximately equal to the cauda. The "*Physiculus*" group has a spindle-type otolith and includes two sub-groups: the "*Physiculus*" subgroup with four genera, *Physiculus*, *Gadella*, *Salilota* and *Tripterophycis*, characterized by the presence of a ventral light organ; and the "*Laemonema*" subgroup with *Laemonema* (including *Guttigadus*), *Microlepidium*, *Podonematichthys*, and *Momonatira*. This subgroup does not have a ventral light organ, but Paulin (1989) indicated these fishes have deeply pigmented tissue around the abdominal area that may be luminescent.

There are several additional genera not treated by Paulin, but relevant to this study. Trunov (1990) described a new genus *Paralaemonema* with three new species, *P. nudicephalum*, *P. nudirostre* and *P. squamirostre*, which he indicated are related to *Laemonema* and *Guttigadus*. There are also six genera, *incertae sedis*. One based on adult (*Austrophycis* and also as outgroup) and two based on juveniles (*Svetovidovia* and *Laemonemodes*). One of the juvenile forms, Svetovidovia, was tentatively referred to Laemonema by Fahay and Markle (1984).

The nomenclature, definition and content of Laemonema are also problematic. The authority for the genus name and the correct type species were confounded by almost simultaneous publication in 1862. In June 1862, Johnson described a new species from Madeira, Laemonema robustum, which he referred to Günther's genus Laemonema. However, it was five months later that Günther described Laemonema based on Phycis yarrelli Lowe, 1841. Since then, 20 nominal species of Laemonema have been described, and two species have been re-assigned to Laemonema.

Günther's (1862) definition of Laemonema and its separation from Phycis was based principally on the low number of first dorsal rays, 5, compared to 8-10 in Phycis. Later, however, Günther (1887) stated that "this group scarcely deserves generic separation from Phycis, it was distinguished only in order that we might be consistent in the employment of certain technical characters, by which the Gadidae have been divided."

Later, Gilchrist (1903) created a new genus Laemonemodes, for those Laemonema having pelvic fins with two long rays plus six minute rays. Norman (1966) although not in a valid publication, synonymized Laemonemodes with Laemonema by amending the generic diagnosis as follows: "...with or without some minute inner rays in pelvic fin." This is an important characteristic, because the description of Laemonemodes was based on an approximately 60 mm standard length (SL) individual. Fahay and Markle (1984) stated that there was a reduction in the number of pelvic rays in a series of Svetovidovia vitellius, which they suggested was probably a juvenile stage of Laemonema.

Holt and Byrne (1908), in their description of Laemonema latifrons, stated that the genus Laemonema required revision. Rass (1954) noted the need for a revision of the genus Laemonema and proposed that the species in the genus Laemonema naturally form two distinct groups. One group, including L. yarrelli (Lowe), L. robustum Johnson, L. barbatulum Goode and Bean, L. gracillipes Garman, and L. rhodochir Gilbert, is distinguished by a protruding upper jaw, a chin barbel, and narrow interorbital space (< 1/4 head length). The other group, L. latifrons Holt and Byrne and L. globiceps Gilchrist, has subequal jaws, a rudimentary or no barbel, and a wide interorbital (> 1/3 head length). Taki (1953) proposed a new subgenus Guttigadus, based on L. nana, and Rass (1954), erected the genus Podonema for Laemonema longipes Shmidt without a complete revision of the genus. Later, Whitley (1965) indicated that Podonema was preoccupied and proposed Podonematichthys as a replacement name.

The Laemonema subgroup as defined by Paulin (1989), plus Paralaemonema, herein called Laemonema sensu lato, is mainly a genus of the continental slope and is distributed in almost all oceans from approximately 54°S to 56°N. Fossil evidence of Laemonema sensu lato comes mainly from otoliths and dates at least to the Miocene (Nolf and Steurbaut 1989). The shallowest species is Laemonema nana, which lives in 25-60 m off Japan. The deepest record is around 1900 m for both Laemonema latifrons (IOS 51021) in the Celtic Sea (Eastern North Atlantic Ocean) and Laemonema longipes in the western North Pacific (Pautov 1980). The purpose of this thesis is to revise the taxonomy of Laemonema sensu lato and to examine its zoogeography based on a cladistic analysis.

MATERIALS AND METHODS

Materials

All nominal species of Laemonema sensu lato are treated as the ingroup. At least one specimen of each recognized species was examined except for Guttigadus nudirostre (Trunov, 1990), G. squamirostre (Trunov, 1990), and L. yuvto Parin and Sazonov, 1990. The morids Austrophycis marginatus (Günther, 1878), Lepidion eques Günther, 1887, Lotella fernandeziana Rendhal, 1921, and Physiculus fulvus Bean, 1884, were selected as out-groups. The selection of the out-groups follows the groups of Paulin (1989) and were limited by availability of specimens.

Institutional abbreviations for material examined follow Leviton et al. (1985). For each species, the museum catalog number, number of specimens, size range (in SL or HL), latitude and longitude, depth, capture date, and type designation (if appropriate) are presented.

Methods

Morphometric and meristic characters were measured according to Hubbs and Lagler (1954), Paulin (1983), and Markle and Meléndez (1988); abbreviations of measurements and counts of the characters follows each measurements. The morphometric characters were: head length (HL), snout length (SNT), barbel length (BARBEL), orbit diameter (ORB), interorbital width (INT), maxillary (UJL), predorsal length

(PDL), first dorsal fin height (D1H), second dorsal fin length (D2L), preanal fin length (PAL), preanus length (PANUS), anal fin length (AL), body depth at base of first anal ray (BD-IA), postorbital length (POSTOR), prepectoral fin length (PREPECT), prepelvic fin length (PREPELVIC), pelvic fin ray length (PELVRAYL), pectoral fin ray length (PECTRAYL), first dorsal fin base length (D1BASE), pectoral fin base length (PECTBASE), maximum body depth (MAXDEPTH), minimum caudal peduncle depth (CAUDDEPTH), and body depth at anus (DEPTHANUS). Morphometric characters were not measured in specimens that were shrunk or in bad condition.

The meristic characters were: first dorsal fin rays (D1), second dorsal fin rays (D2), anal fin rays (A), pectoral fin rays (P1), pelvic fin rays (P2), precaudal vertebrae (PCV), caudal vertebrae (CV), total vertebrae (TV), lower gill rakers (LGR), upper gill rakers (UGR), total gill rakers (TGR), upper procurrent caudal fin rays (UPPCR), principal caudal fin rays (PCR), lower procurrent caudal fin rays (LPCR), scales above lateral line (SALL), and scales below lateral line (SBLL). Generally, lateral line scale counts were difficult to make and lateral body scale counts, taken along the lateral midline were recorded (LL). Meristic characters were taken directly from the specimen or from dissected, cleared and stained (Potthoff 1984), or x-rayed individuals. Abbreviations used in the figures are presented in Appendix 1.

Specimens with a regenerated caudal fin were not counted, because only principal caudal rays are regenerated in morids.

Single and multiple-character analyses were used for discriminating species. For single-character analyses of morphometric and meristic data, mean, range, mode, standard deviation, and coefficient of variation (Templeman 1970; Paulin 1983; Chiu 1987; Wiley 1981; Iwamoto and Sazonov 1988, and Walker and Rosenblatt 1988) were used to discover diagnostic or "key" characters. Comparisons between descriptive statistics were based mainly on Student's t-test (for two species), (Mayden 1988; McEachran and Miyake 1988). A 95 % confidence level was accepted for diagnostic characters (Templeman 1970; Mayden 1988). Multivariate character analysis included scatter plots, regression analysis, principal-component-analysis, and discriminant analysis, (Wiley 1981; Barbour and Chernoff 1984; McEachran and Miyake 1988). Analyses were performed with Statgraphics version 7.0 (Manugistic Inc. and Statistical Graphics Corporation 1993).

To determine if larvae and juveniles of <u>Svetovidovia</u> specimens are <u>Laemonema</u>, the approach given by Powles and Markle (1984) was used. The approach is to work backwards from adult specimens utilizing characters common to successively earlier ontogenic stages, tempered by knowledge of the adult taxa found in the study area.

A cladistic approach to phylogenetic reconstruction, following Hennig (1966), was used to determine if Laemonema is a monophyletic group. Anatomical structures analyzed were caudal skeleton, gill arches, pectoral and pelvic girdle, hyomandibular bone, first pterygiophore of first dorsal fin, maxillary, number of precaudal vertebrae opposite the first anal ray, and external structure and shape of gas bladder. Dissection of gill arches and hyomandibular bone followed Weitzman (1974). Figures of anatomical characters were prepared using a camera lucida, with cartilage represented by stippled pattern.

The use of selected meristic and morphometric characters for cladistic analysis follows Mayden et al. (1991), in which the average and standard deviation were obtained for each meristic and morphometric (as % SL) character. The selection of morphometric characters was made by plotting each character against SL for all species. Those characters that showed more variation were considered; for example, characters showing possibilities for separating two or more groups, or had different regression slopes, were selected (Fig. 1).

Gap coding of meristic characters follows Baum (1988). The standard deviation of each meristic character selected for each species was added to and subtracted from the average, obtaining a range with minimum, midpoint (average), and maximum value. Each character for the studied species was ranked according to its minimum and maximum value and

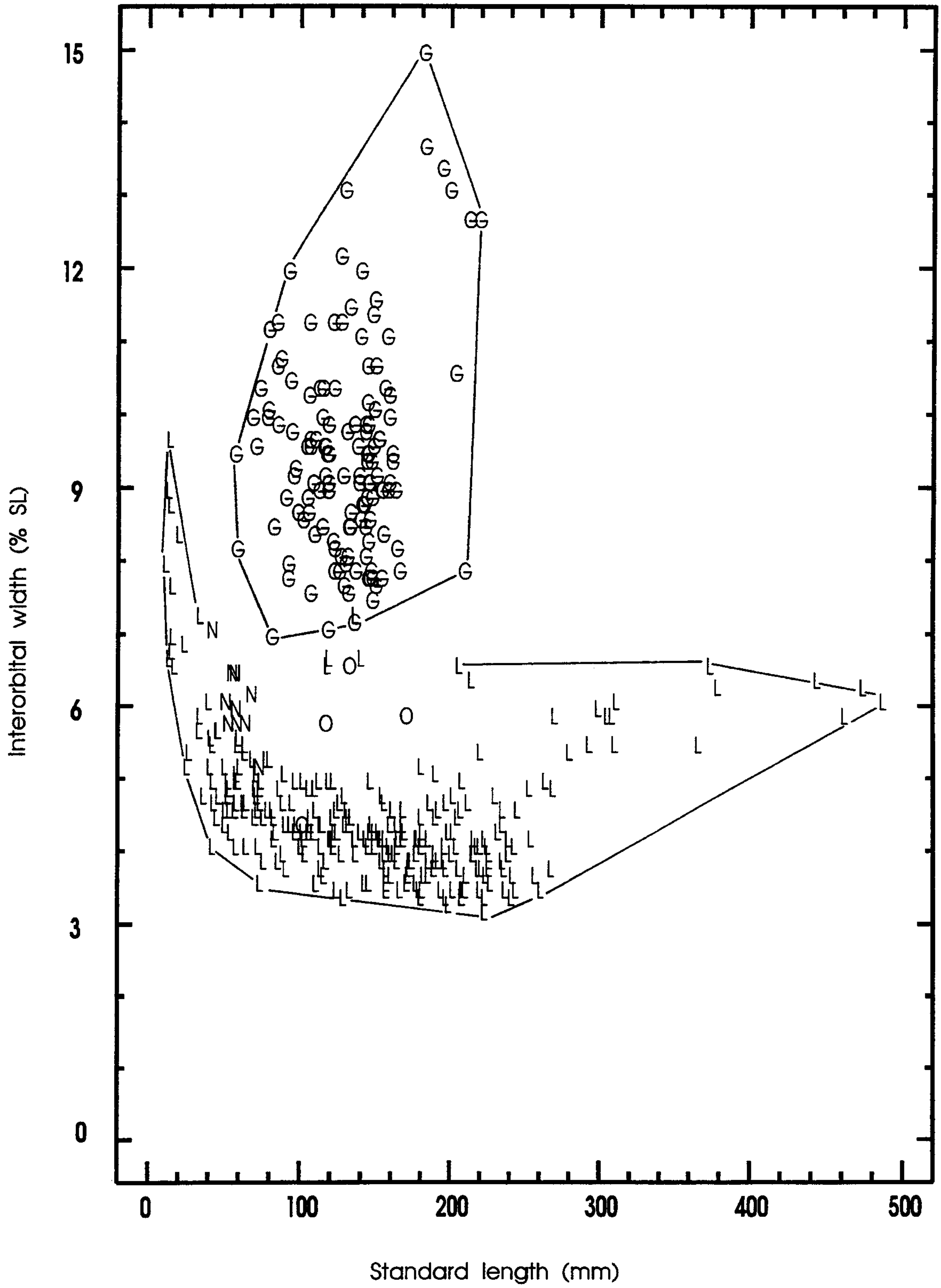


Fig. 1. Interorbital width (%SL) vs Standard length (mm) for Laemonema sensu lato (G=Guttigadus, L=Laemonema, N=G. nana, and O=Outgroups).

this ranking was plotted for each species. Species with similar minimum and maximum values were grouped together, then assigned codes 0 to n (n<9) where the n's represent identical minimum and maximum values. The code 0 was assigned to the plesiomorphic character, according to outgroup analysis. Code 9 was assigned to either missing data or no character state.

Polarity of character states was determined by out-groups, and followed Watrous and Wheeler (1981) and Maddison et al. (1984). Essentially, characters with one or more states found in both outgroup and ingroup species were considered plesiomorphic. Because the interrelationship of the outgroups with the ingroup are not well corroborated, and the most recent or sister out-group is unknown, the outgroup node will be equivocal for characters in which the four outgroup representatives have different states. If available, data about polarization of the character was taken from the literature (e.g., Markle 1989). Morid fishes are poorly studied phylogenetically, so the polarity of characters is difficult to determine. Ontogeny was used to help polarize pelvic fin ray counts following Nelson's (1978) logic: a character that changes from larvae to adults will have the larval state coded as plesiomorphic. This contrasts with the approach of Fahay and Markle (1984), who considered the ontogeny itself the character with states such as "ontogenetic increase in pelvic fin rays" or "ontogenetic decrease in pelvic fin rays". The absence of ontogenetic information for most species precludes the use of these types of characters.

Phylogenetic data were analyzed with the software PAUP (Phylogenetic Analysis Using Parsimony) version 3.0 (Swofford 1991), and Mac Clade version 3.0 (Maddison and Maddison 1992). In PAUP, the data were analyzed with the Heuristic-search and Branch-and-Bound options. Mac Clade was used to observe each character studied, using the trace tool.

RESULTS

Classification

In order to facilitate presentation of results, the classification used is presented first. Evidence for the arrangement is found in subsequent sections.

Laemonema Günther, 1862

Laemonema barbatulum Goode and Bean, 1883

Laemonema n.sp. g

Laemonema gracillipes Garman, 1899

Laemonema n.sp. i

Laemonema laureysi Poll, 1953

Laemonema longipes (Shmidt, 1939)

Laemonema melanurum Goode and Bean, 1896

Laemonema rhodochir Gilbert, 1905

Laemonema robustum Johnson, 1862

Laemonema verecundum (Jordan and Cramer, 1897)

Laemonema yarrelli (Lowe, 1841)

Laemonema yuvto Parin and Sazonov, 1990

Guttigadus Taki, 1953

Guttigadus globiceps (Gilchrist, 1906)

Guttigadus globosus (Paulin, 1983)

Guttigadus kongi (Markle and Meléndez, 1989)

Guttigadus latifrons (Holt and Byrne, 1908)

Guttigadus nana Taki, 1953

Guttigadus nudicephalum (Trunov, 1990)

incertae sedis (not treated in phylogenetic analysis)

Guttigadus nudirostre (Trunov, 1990)

Guttigadus squamirostre (Trunov, 1990)

Laemonemodes compressicauda Gilchrist, 1903

Phylogenetics analysis

Morphometric and meristic data:

The characters used in the cladistic analysis are numbered and summarized in Table 1. In the following text, the character number is placed in bold type in parentheses following initial mention. Values of morphometric and meristic characters used in the analysis (Table 2) and the ranges of the characters (Table 3) are summarized for easy reference. The data matrix used for cladistic analysis is shown in Table 4.

The interorbital width (**1**) of specimens greater than 50 mm was coded with two states, state 0 was narrow (3.0-7.0 % SL), the plesiomorphic state, and state 1 was wide (7.1-15.0 % SL) (Table 4). Two species L. melanurum and L. barbatulum represented by large sample sizes that included young "Svetovidovia" stages showed a decrease in relative interorbital width (from about 7-10% in L. melanurum smaller than 50 mm, to about 5% in larger specimens). Guttigadus, except G. nana, have a wide interorbital, the derived state, and all other taxa, including the outgroups, have a narrow interorbital (Fig. 1 and Table 4). The regression

Table 1.- List of meristic and anatomical character used for cladistic analysis.

1.- Interorbital width.
2.- Principal Component analysis of D1, A, PCV and CV.
3.- Number of pectoral fin rays.
4.- Number of lower gill rakers.
5.- Presence or absence of highly modified scales on lateral line.
6.- Presence or absence of the first phraryngobranchial.
7.- Presence or absence of the second pharyngobranchial.
8.- Number of articulations on pharyngobranchial two.
9.- Presence or absence of the uncinate process in the first epibranchial.
10.- Presence or absence of the interarcual cartilage.
11.- Presence or absence of the interarcual ligament.
12.- Length of the first epibranchial related to the second epibranchial.
13.- Third pharyngobranchial with a presence or absence of a groove on the strut 3 and 4.
14.- Shape of the joining cartilage of the superior arms of the pelvic girdle.
15.- Angle between superior and inferior arms on each side of pelvic girdle.
16.- Presence or absence of a foramen on pelvic girdle
17.- Number of visible pelvic fin rays.
18.- Length of the third pelvic ray related with the largest ray of the pelvic fin.
19.- Total number of pelvic fin rays in adults.
20.- Presence or absence of a "neck" between chambers in the swim bladder.
21.- Number of parapohyses in the second chamber of the swim bladder.
22.- Presence or absence of a ligament between swim bladder and cranium.
23.- Cornua of the first chamber of the swim bladder attached or not to the skin.
24.- Type of cornua of the swim bladder.
25.- Presence or absence of a foramen on scapula and coracoid bones.
26.- Length of the coracoid arm.
27.- Width of the cartilagenous tip of the coracoid arm.
28.- Size of the teeth on upper jaws.
29.- Number of teeth on upper jaws.
30.- Shape of the maxillary process.
31.- Presence or absence of a posterior notch between the maxillary process and maxillary.
32.- Presence or absence of Vomer.
33.- Number of teeth on vomer.
34.- Shape of vomer.
35.- Ratio between length of the hyomandibular bone and length of its opercular arm.

Table 2.- Continued....

36.- Presence or absence of an antero-lateral blade of the hyomandibular bone.
37.- Position of the foramen in the hyomandibular bone.
38.- Length of the supero-posterior blade of the hyomandibular bone.
39.- Length of the antero-inferior blade of the hyomandibular bone.
40.- Number of the upper procurrent caudal fin rays.
41.- Number of the lower procurrent caudal fin rays.
42.- Number of preural vertebrae opposite to the first upper procurrent caudal fin ray.
43.- Number of preural vertebrae opposite to the first lower procurrent caudal fin ray.
44.- Position of anus related to the beginning of the anal fin.
45.- Presence or absence of a laminar bone on the first pterygiophore of the first dorsal fin.
46.- Number of the precaudal vertebrae opposite at the level of the first anal fin ray.
47.- Presence or absence of a black stripe along the first and second dorsal fin.
48.- Base of the vertical fin fleshy.
49.- Living depth.

Table 2.- Average (X) and standard deviation (s) for percentage of morphometric (in SL) and meristic character used in phylogenetic analysis of morids fishes studied (*=outgroups).

Species	Morphometric		Meristic Character			
	INT		P1		LGR	
	X	s	X	s	X	s
L. barbatulum	4.6	0.39	21.1	0.76	11.5	0.59
L. n.sp. g	4.0	0.37	20.2	0.72	18.3	0.83
L. gracillipes	4.8	0.35	22.2	0.75	18.0	1.90
L. n.sp. i	4.8	0.21	27.0	0.00	12.3	0.58
L. laureysi	3.8	0.33	20.8	0.85	18.5	0.96
L. longipes	6.5	0.35	16.9	0.79	19.8	0.96
L. melanurum	4.8	0.26	26.2	0.98	13.2	1.16
L. modestum	4.9	0.00	27.0	0.00	13.0	0.00
L. rhodochir	4.3	0.31	22.7	0.75	12.5	0.88
L. robustum	5.5	0.42	27.8	1.11	14.0	0.94
L. verecundum	4.2	0.46	18.7	0.47	13.0	0.82
L. yarrelli	4.3	0.43	22.9	1.14	16.2	0.84
L. yuvto	5.1	0.00	31.0	0.00	13.0	0.00
G. globiceps	9.3	0.92	19.1	2.53	25.8	2.56
G. globosus	12.5	1.00	24.6	0.78	18.1	0.87
G. kongi	9.6	1.47	24.1	1.23	16.4	1.95
G. latifrons	8.7	0.69	22.1	1.16	15.8	0.85
G. nana	6.1	0.51	23.2	0.60	4.7	0.65
G. nudicephalum	10.1	0.98	27.6	0.55	10.4	0.55
A. marginatus	* 4.4	0.00	22.0	0.00	18.0	0.00
Le. eques	* 5.8	0.00	22.0	0.00	14.0	0.00
Lo. fernandeziana	* 5.9	0.00	24.0	0.00	8.0	0.00
P. fulvus	* 6.6	0.00	24.0	0.00	8.0	0.00

Table 3.- Summary of meristic ranges for the studied species

Species	Meristic Ranges			
	D1	D2	A	P1
L. barbatulum	6 - 7	57 - 63	54 - 63	19 - 23
L. n. sp. g	6	66 - 73	65 - 71	19 - 22
L. gracillipes	6	56 - 63	55 - 61	21 - 23
L. n. sp. i	6	57 - 58	54 - 55	27
L. laureysi	5 - 7	63 - 72	60 - 69	19 - 23
L. longipes	6	49 - 53	48 - 52	16 - 18
L. melanurum	7	53 - 61	52 - 59	25 - 27
L. rhodochir	6	61 - 66	58 - 63	22 - 24
L. robustum	6	50 - 57	48 - 54	26 - 30
L. verecundum	8 - 9	40 - 42	41	18 - 19
L. yarrelli	6	58 - 62	57 - 62	21 - 25
L. yuvto	6	62	53	31
G. globiceps	4 - 7	65 - 77	60 - 74	18 - 21
G. globosus	4 - 6	70 - 86	73 - 84	23 - 29
G. kongi	4 - 7	62 - 78	61 - 75	22 - 27
G. latifrons	5 - 6	64 - 76	61 - 76	21 - 26
G. nana	4 - 6	45 - 54	46 - 53	22 - 24
G. nudicephalum	4 - 5	59 - 62	56 - 60	27 - 28

Table 3.- continued...

Species	Meristic Ranges			
	PCV	CV	TV	UGR
L. barbatulum	13 - 15	37 - 42	50 - 56	3 - 6
L. n. sp. g	15 - 17	39 - 43	56 - 59	7 - 9
L. gracillipes	15 - 16	37 - 38	52 - 54	6 - 8
L. n. sp. i	14	35 - 37	49 - 51	4 - 5
L. laureysi	14 - 17	38 - 43	53 - 58	5 - 8
L. longipes	14 - 16	34 - 37	49 - 52	7 - 8
L. melanurum	15 - 16	38 - 42	53 - 57	4 - 6
L. rhodochir	15	36 - 39	51 - 54	4 - 6
L. robustum	13 - 15	34 - 38	47 - 52	4 - 7
L. verecundum	12 - 13	29 - 31	42 - 43	5 - 6
L. yarrelli	15 - 16	36 - 38	52 - 54	6 - 8
L. yuvto	15	36	51	5
G. globiceps	11 - 13	44 - 50	55 - 62	10 - 13
G. globosus	12 - 14	42 - 47	56 - 59	6 - 8
G. kongi	10 - 13	37 - 44	49 - 56	6 - 10
G. latifrons	10 - 13	41 - 49	54 - 61	7 - 8
G. nana	10 - 12	27 - 30	39 - 41	1 - 2
G. nudicephalum	12 - 13	36 - 38	48 - 51	3 - 5

Table 3.- continued...

Species	Meristic Ranges			
	LGR	UPPCR	LPCR	LL
L. barbatulum	10 - 13	7 - 9	14 - 20	128 - 140
L. n. sp. g	17 - 20	8 - 11	12 - 16	125 - 143
L. gracillipes	16 - 21	8 - 9	12 - 14	155 - 172
L. n. sp. i	12 - 13	8	11 - 13	125 - 126
L. laureysi	16 - 21	7 - 10	10 - 15	120 - 140
L. longipes	18 - 20	7 - 8	9 - 11	110 - 144
L. melanurum	12 - 15	7 - 10	11 - 15	145 - 166
L. rhodochir	11 - 14	7 - 10	11 - 13	105 - 130
L. robustum	13 - 16	10 - 12	12 - 17	120 - 150
L. verecundum	12 - 14	11	13	no data
L. yarrelli	14 - 18	6 - 7	11 - 12	100 - 111
L. yuvto	13	no data	no data	135
G. globiceps	22 - 30	7 - 9	9 - 12	85 - 105
G. globosus	17 - 20	10 - 12	13 - 15	111 - 137
G. kongi	13 - 21	8 - 12	10 - 14	170
G. latifrons	14 - 17	10 - 12	12 - 14	145 - 150
G. nana	4 - 6	7 - 8	9 - 10	60 - 75
G. nudicephalum	10 - 11	11 - 12	12 - 14	114 - 135

Table 3.- continued...

Species	Meristic Ranges	
	SALL	SBLL
L. barbatulum	12 - 15	21 - 30
L. n. sp. g	10 - 13	no data
L. gracillipes	14 - 15	30 - 35
L. n. sp. i	10 - 11	23 - 24
L. laureysi	10 - 13	22
L. longipes	10 - 11	20 - 25
L. melanurum	18	35 - 36
L. rhodochir	9 - 15	21
L. robustum	14 - 19	39 - 47
L. verecundum	no data	no data
L. yarrelli	8 - 9	18 - 23
L. yuvto	13	no data
G. globiceps	7 - 8	15 - 25
G. globosus	12	27
G. kongi	12	35
G. latifrons	14	38
G. nana	8	no data
G. nudicephalum	18 - 20	40 - 55

Table 4.- Data matrix for cladistic analysis (* = outgroups)

Taxa		Characters				
		1	1111111112	2222222223	3333333334	444444444
		1234567890	1234567890	1234567890	1234567890	123456789
L. barbatulum		0001000001	1100002200	0100001101	0100101111	010011010
L. n.sp. g		0001000001	0100002200	0100000001	1100001111	110010000
L. gracillipes		0001000101	1100002200	9100000001	0110001011	100090000
L. n. sp. i		0011000001	0110012201	0101001011	0100001111	110001000
L. laureysi		0001000001	0100002200	0100000001	1100001010	100010000
L. longipes		0001001011	1100102212	9111100010	2101111011	101011000
L. melanurum		0011000001	1100002200	0100101001	0100001011	100010000
L. rhodochir		0001000101	0100002200	0100001011	0100001011	111010000
L. robustum		0011000101	1010012201	0101001011	0110101010	100010000
L. verecundum		0001000001	1100001212	9110001010	2101001000	199091000
L. yarrelli		0001000001	1100002200	0100000001	0100101011	110010010
L. yuvto		0011199999	9999992299	9999999099	9190999999	999199000
G. globiceps		1102110010	0101001210	1000011000	1100111111	111101100
G. globosus		1101100011	1001101110	1000011000	1100111010	100111100
G. kongi		1101100010	1101101110	1000011100	1100111010	100111100
G. latifrons		1101100000	0001001110	1000111000	1100111110	100101100
G. nana		0200012910	0000101212	9001110000	0099100111	111001001
G. nudicephalum		1111100010	0001101110	1100011200	1111111110	100111100
Lo. fernandeziana	*	0000000010	0100000000	0001001201	0099100000	000010001
A. marginatus	*	0001001010	0000001110	0000010000	0099000000	000010000
Le. eques	*	0001010001	1100000000	0100111001	0110111100	000020000
P. fulvus	*	0000000000	1001000000	0000000010	1099000111	111011000

relationship of interorbital width on standard length (50-250 mm) was: Laemonema (INT=0.8+0.04SL, N=260, r^2=0.86); G. nana (INT=1.4 + 0.04SL, N=9, r^2=0.72); and Guttigadus (INT=2.6+0.12SL, N=133, r^2=0.73). Although the sample size for G. nana was small, the identity of the slopes of Laemonema spp. and G. nana suggest that the two have a similar ontogeny of this character.

Four meristic characters were found to be correlated: number of second dorsal fin rays, number of anal fin rays, number of precaudal vertebrae, and number of caudal vertebrae (**2**, Fig. 2). In order to avoid redundancy, the four characters were analyzed in a Principal Component Analysis (Fig. 3). Three groups were found; Laemonema and the outgroups fell together and were coded as state 0; most Guttigadus fell together and were coded state 1; and G. nana was separate, coded state 2. The character-state change from the Laemonema condition is a synapomorphy for all Guttigadus.

A low number of pectoral fin rays (**3**) (16-24), as found in all outgroups, was plesiomorphic, state 0, and a higher number (25-31) was derived, state 1 (Table 4). The derived state of a higher number of pectoral fin rays tended to be found in those Laemonema with a deep body, and the lower numbers in those with a narrow body. In Guttigadus this trend was not present.

A low number of gill rakers (4-8) on the lower limb of the first arch (**4**) was state 0, an intermediate number (9-

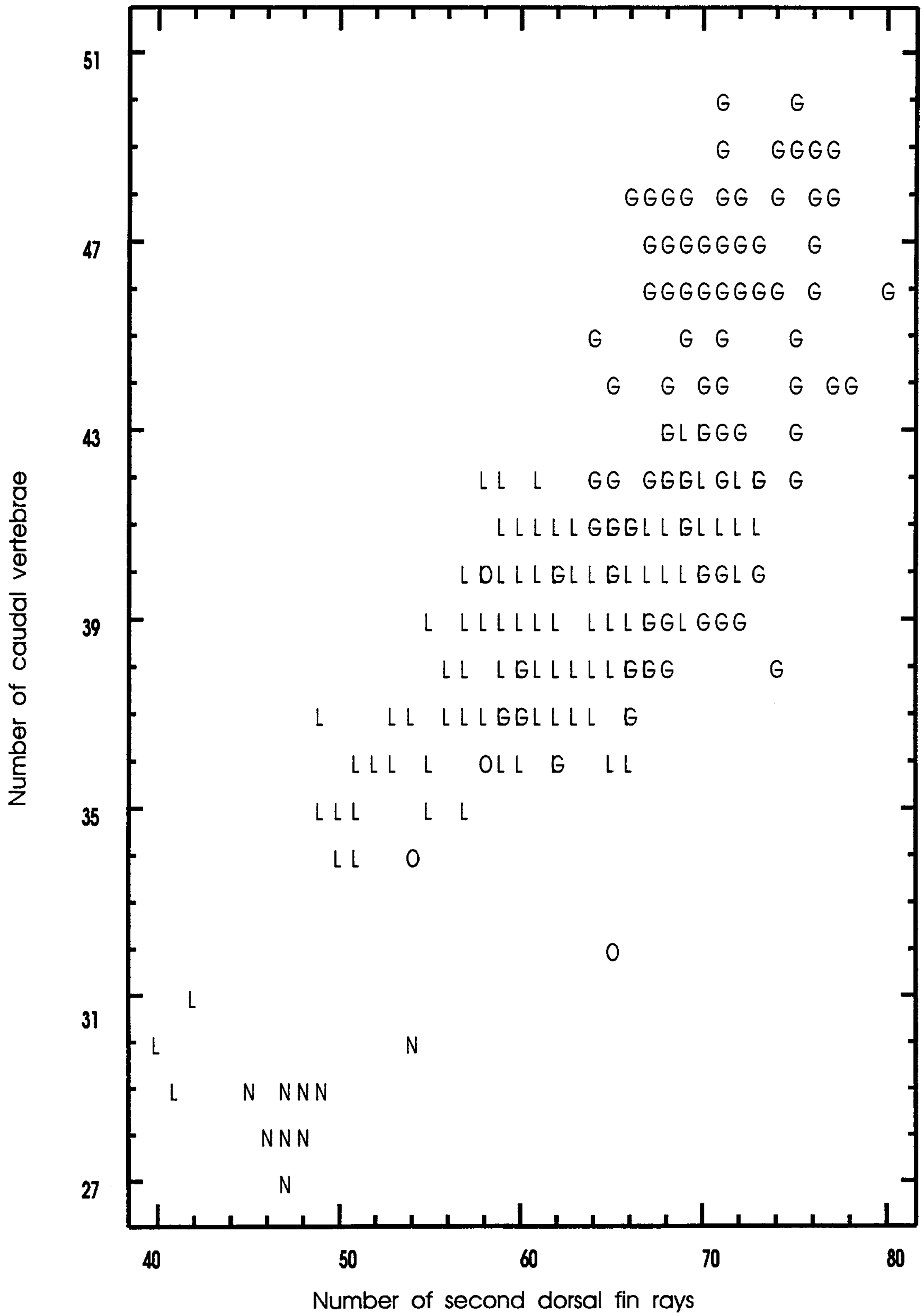


Fig. 2. Number of caudal vertebrae vs Number of second dorsal fin rays (G=Guttigadus, L=Laemonema, N=G. nana, and O=Outgroups).

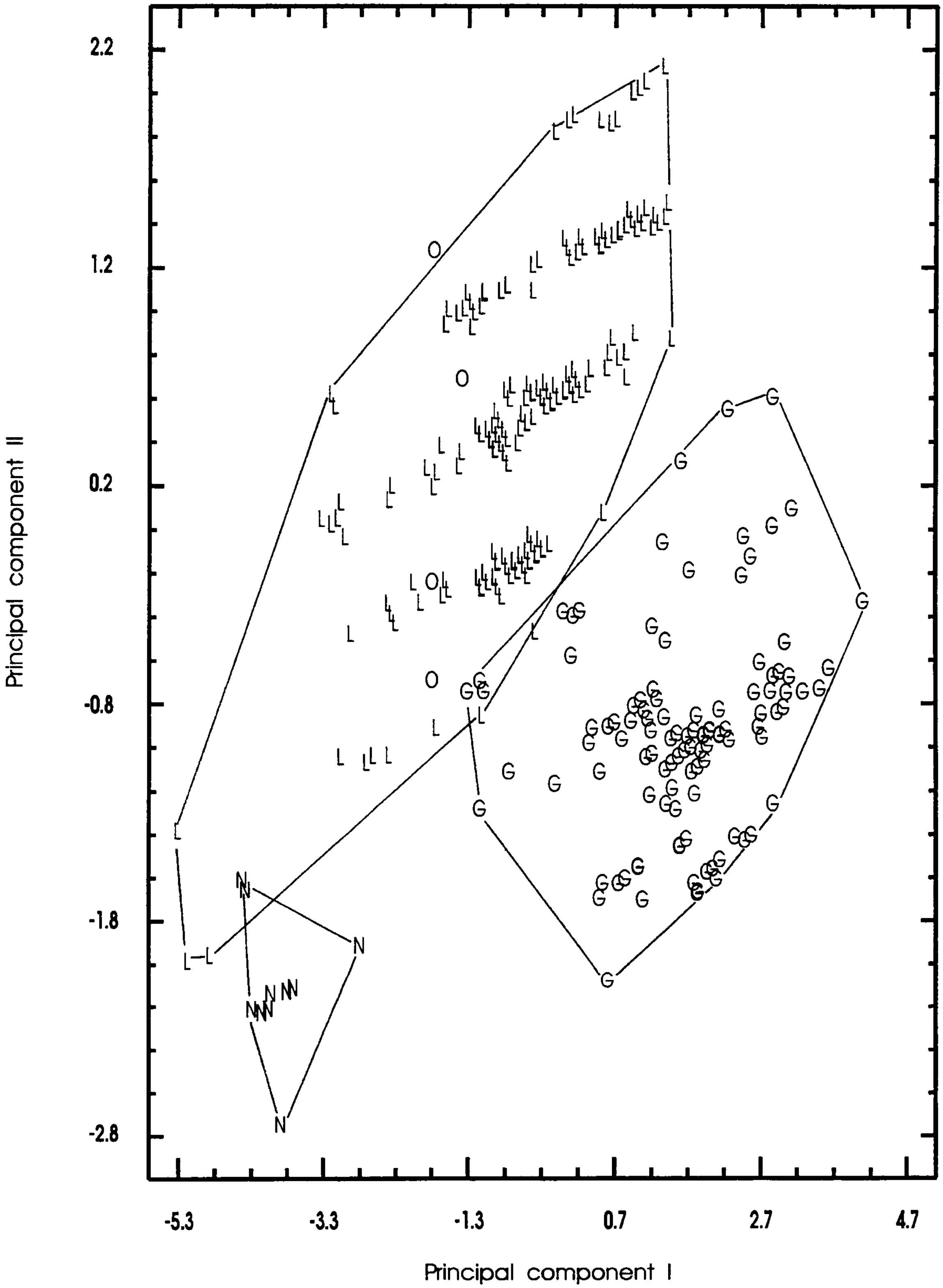


Fig. 3. Principal component analysis for meristic characters for Laemonema sensu lato (G=Guttigadus, L=Laemonema, N=G. nana, and O=Outgroups).

21) was state 1, and a high number (more than 21) was state 2 (Tables 2 and 3). The outgroup analysis was equivocal (Table 4). This character does not vary much, only G. globiceps (22-30 LGR) and G. nana (4-6 LGR) were scored differently than other Laemonema and Guttigadus. The reduction in G. nana is similar to the reduction in serial meristic characters noted for **2** above.

Osteological and anatomical characters (Table 1):

Scales:

Two character states were identified for scale type on the lateral line (**5**), one type was little modified, state 0, and the other was highly modified, state 1. All outgroups had the plesiomorphic state (Table 4). The highly modified scales form a small tube surrounded by skin, with a wide opening anteriad, and a taper to small posteriad opening. Each scale supports a tapered, trumpet-shaped segment that is highly pigmented. The pigmentation makes the segments distinct in contrast to the paler body of preserved specimens. These scales seem restricted to Guttigadus (except G. nana) and L. yuvto. We include L. yuvto because Parin and Sazonov (1990) reported "... modified lateral line scales 29-30," and Sazonov (pers. comm, 1995) describes the scales as "tubular." A juvenile of G. kongi (NMNZ P 23396, 57 mm SL) has these modified scales formed, indicating that development began at least by the juvenile stage. The absence of modified scales in G. nana, which reaches a maximum of 73.1 mm SL, might be interpreted as the absence of a character that develops in late juvenile or early adult stages of ancestral Guttigadus.

Dorsal gill arches:

The gill arch (Figs. 4-5) generally had four epibranchials and four pharyngobranchials. Markle (1989) described selected gadiform gill arch osteology, but he did not describe any morids. The presence of the first pharyngobranchial is variable in gadiforms (Markle 1989) (**6**), its presence scored as state 0 (Figs. 4, 5b) and its absence as state 1 (Figs. 5a, 5c). The outgroup analysis was equivocal because Lepidion eques lacked a first pharyngobranchial (Figs. 5d and Table 4). Both G. nana and G. globiceps also lacked a first pharyngobranchial (Figs. 5a and 5c).

The second pharyngobranchial has three states (**7**): well developed, state 0 (Figs.4a-c); small, state 1 (Fig. 4d); and absent, state 2 (Fig. 5a). The outgroup analysis for this character was equivocal (Figs. 5d-5e and Table 4). The only species without a second pharyngobranchial was G. nana.

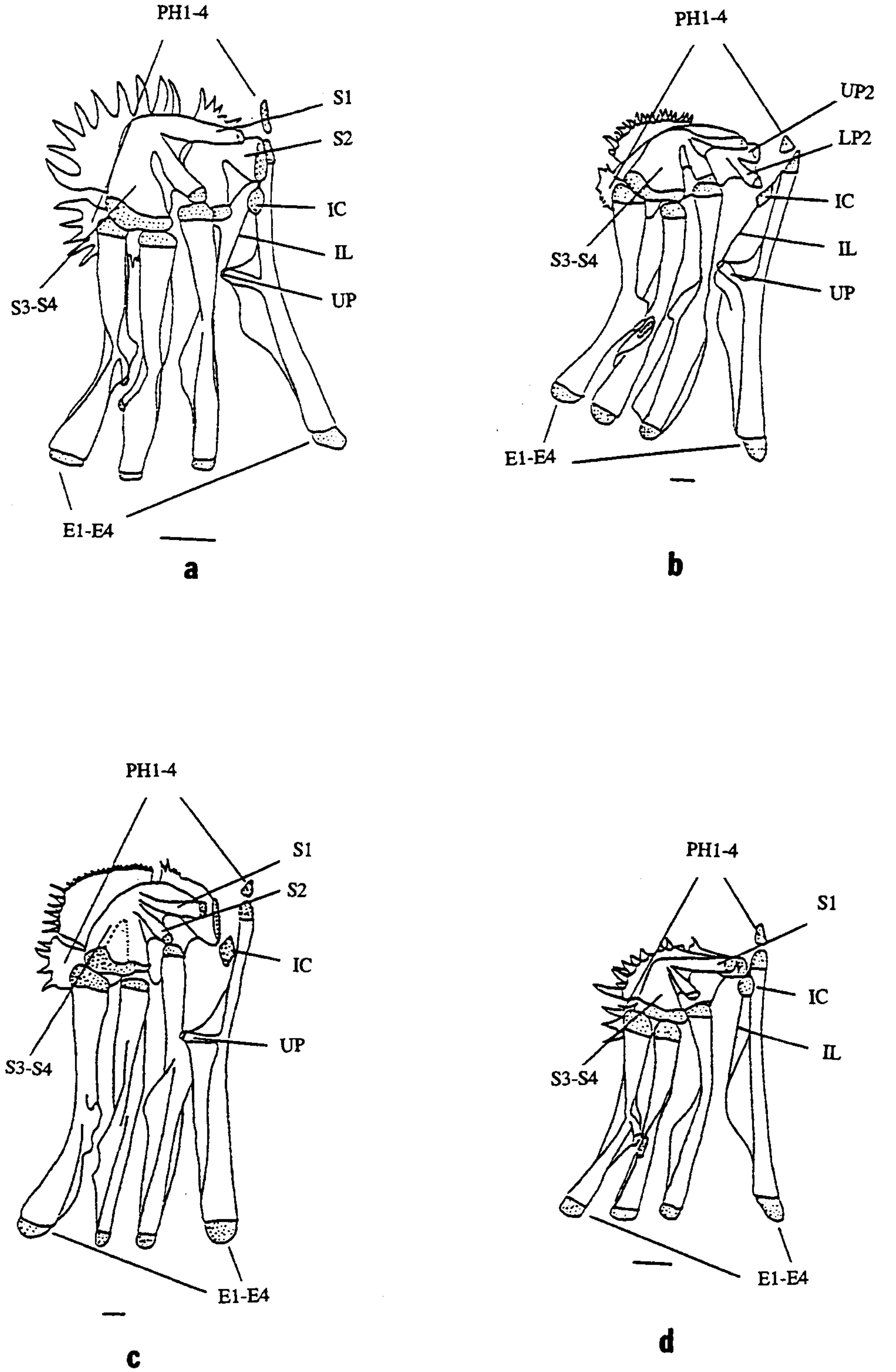
The presence of one upper articulation in pharyngobranchial two (**8**) (Figs. 4a, 4c-d, 5b-c), was considered as plesiomorphic, state 0, the presence of two upper articulations (Figs. 4b) was considered derived, state 1. Because of the absence of the pharyngobranchial two in G.

Fig. 4a.- Dorsal view of the right dorsal gill arch of _Laemonema_ _barbatulum_ (UF 13120). Scale = 1 mm

Fig. 4b.- Dorsal view of the right dorsal gill arch of _Laemonema_ _gracillipes_ (USNM 135362). Scale = 1 mm

Fig. 4c.- Dorsal view of the right dorsal gill arch of _Laemonema_ n.sp. i (RUSI 1423). Scale = 1 mm

Fig. 4d.- Dorsal view of the right dorsal gill arch of _Laemonema_ _longipes_ (CAS 47657). Scale = 1 mm


PH1-4
S1
S2
IC
IL
UP
S3-S4
E1-E4
a
PH1-4
UP2
LP2
IC
IL
UP
S3-S4
E1-E4
b
PH1-4
S1
S2
IC
UP
S3-S4
E1-E4
c
PH1-4
S1
IC
IL
S3-S4
E1-E4
d

Figs. 4a-4d

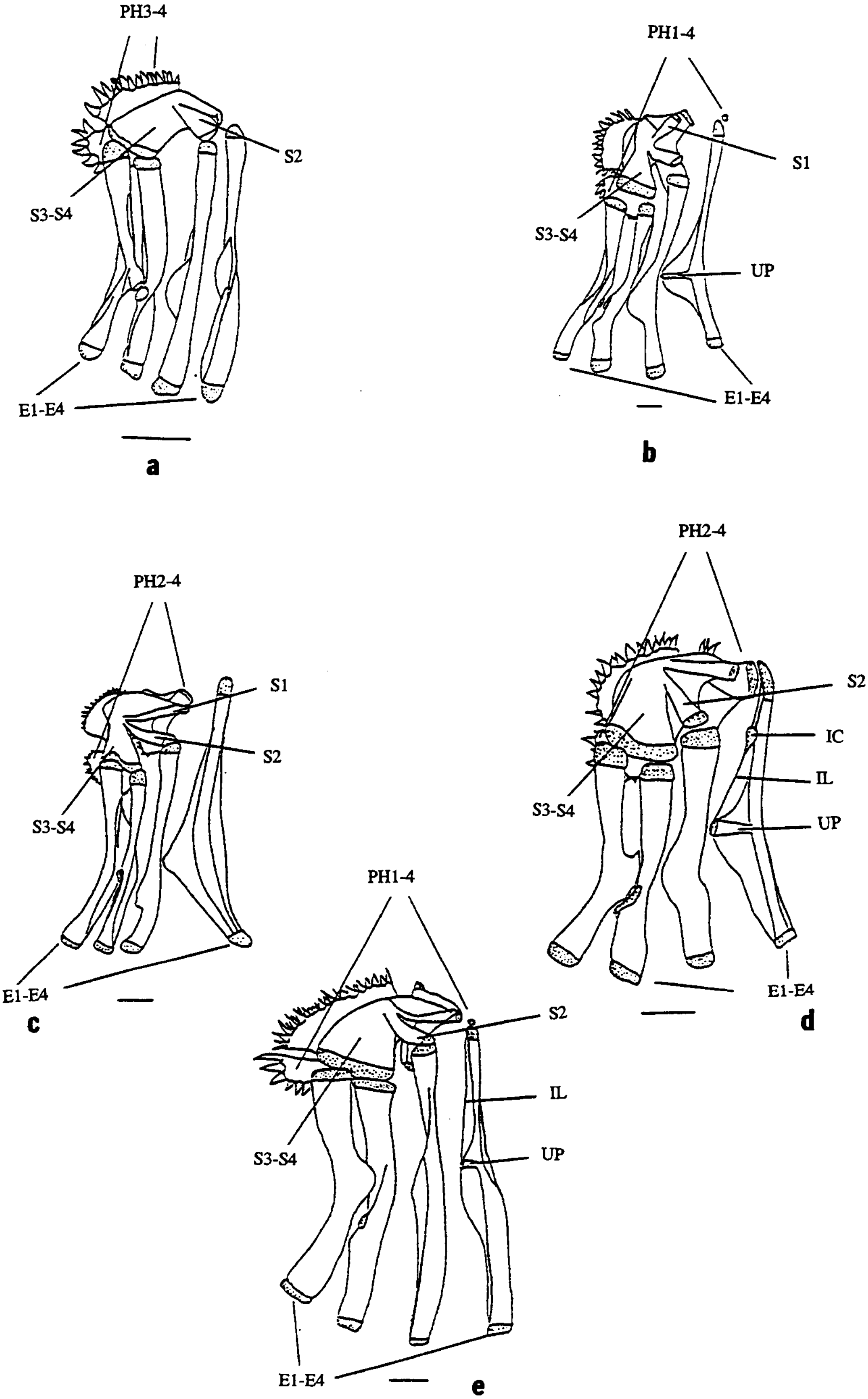
Fig. 5a.- Dorsal view of the right dorsal gill arch of *Guttigadus nana* (UMMZ 214588). Scale = 1 mm

Fig. 5b.- Dorsal view of the right dorsal gill arch of *Guttigadus latifrons* (MSU uncat.). Scale = 1 mm

Fig. 5c.- Dorsal view of the right dorsal gill arch of *Guttigadus globiceps* (MSU uncat.). Scale = 1 mm

Fig. 5d.- Dorsal view of the right dorsal gill arch of *Lepidion eques* (USNM 211787). Scale = 1 mm

Fig. 5e.- Dorsal view of the right dorsal gill arch of *Physiculus fulvus* (USNM 232481). Scale = 1 mm


PH3-4
S2
S3-S4
E1-E4
a
PH1-4
S1
S3-S4
UP
E1-E4
b
PH2-4
S1
S2
S3-S4
E1-E4
c
PH2-4
S2
IC
IL
UP
S3-S4
E1-E4
d
PH1-4
S2
IL
UP
S3-S4
E1-E4
e

Figs. 5a-5e

nana (Fig. 5a), this character was coded as no state, state 9. All outgroups shared the plesiomorphic condition (Figs. 5d-e and Table 4).

There are four epibranchials in all species studied. The first epibranchial may have an uncinate process (**9**), state 0 (Figs. 4a-c, 5b), or not have an uncinate process, state 1 (Figs. 4b, 5a, 5c). The outgroup analysis was equivocal (Figs. 5d-e and Table 4). Markle (1989), indicated that the presence of an uncinate process is a primitive condition for batrachoidiforms fishes which are the out-group of gadiform fishes within paracanthopterygians.

The presence of an interarcual cartilage (**10**), considered a derived state for gadiform fishes (Markle 1989), was absent in some species, state 0 (Figs. 5a-c) and present in others, state 1 (Figs. 4a-d). The outgroup analysis was equivocal (Figs. 5d-e and Table 4). The interarcual cartilage is sustained generally by an interarcual ligament, which is connected with the uncinate process and the nonossified area of the first epibranchial. The interarcual ligament (**11**) was present, state 1 (Figs. 4a, 4d) or absent, state 0 (Figs. 4b-c, 5a-c). The outgroup analysis was equivocal (Figs. 5d-e and Table 4).

Two character states were found for the maximum length of the first epibranchial (**12**), expressed as percentage of the second epibranchial, 90-120 % was state 1 (Figs. 4a-d, 5b) and less than 90% was state 0 (Figs. 5a, 5c). The outgroup analysis was equivocal (Figs. 5d-e and Table 4).

The presence of a groove on strut 3 and 4 (**13**) was a derived state, state 1 (Figs. 5c), found only in L. n.sp. i, and L. robustum; the absence was plesiomorphic, state 0 (Figs. 4a-b, 4d, 5a-c). The outgroup analysis was decisive because all outgroups share the plesiomorphic state (Figs. 5d-e and Table 4).

In the five epibranchial/interarcual characters Laemonema tend to be more conservative and Guttigadus more variable, mainly in reductions or losses of the uncinate process, interarcual cartilage or interarcual ligament. Guttigadus nana again showed the most reductions and losses, possibly indicating neotenic or paedomorphic ancestry.

Pelvic girdle:

The pelvic girdle (Figs. 6a-g) is formed by the basipterygia and has two pairs of arms, the superior arm of which is united to its opposite member by a cartilaginous joint, and a free inferior arm. The cartilaginous joint (**14**) had two states with an anteriorly directed projection, state 0 (Figs. 6a-c, 6e), and without, state 1 (Figs. 6d, 6f). The outgroup analysis was equivocal (Figs. 6g and Table 4). The angle between the two arms (**15**), could be categorized as less than 90° (Figs. 6a-c, 6f), the plesiomorphic condition, state 0, or equal or greater than 90° (Figs. 6d-e), the derived state, state 1. All the outgroups share an angle of less than 90° (Figs. 6g and Table 4).

Fig. 6a.- Dorsal view of a half of the pelvic girdle of Laemonema laureysi (IRSB 175). Scale = 1 mm

Fig. 6b.- Dorsal view of a half of the pelvic girdle of Laemonema n.sp. i (RUSI 1423). Scale = 1 mm

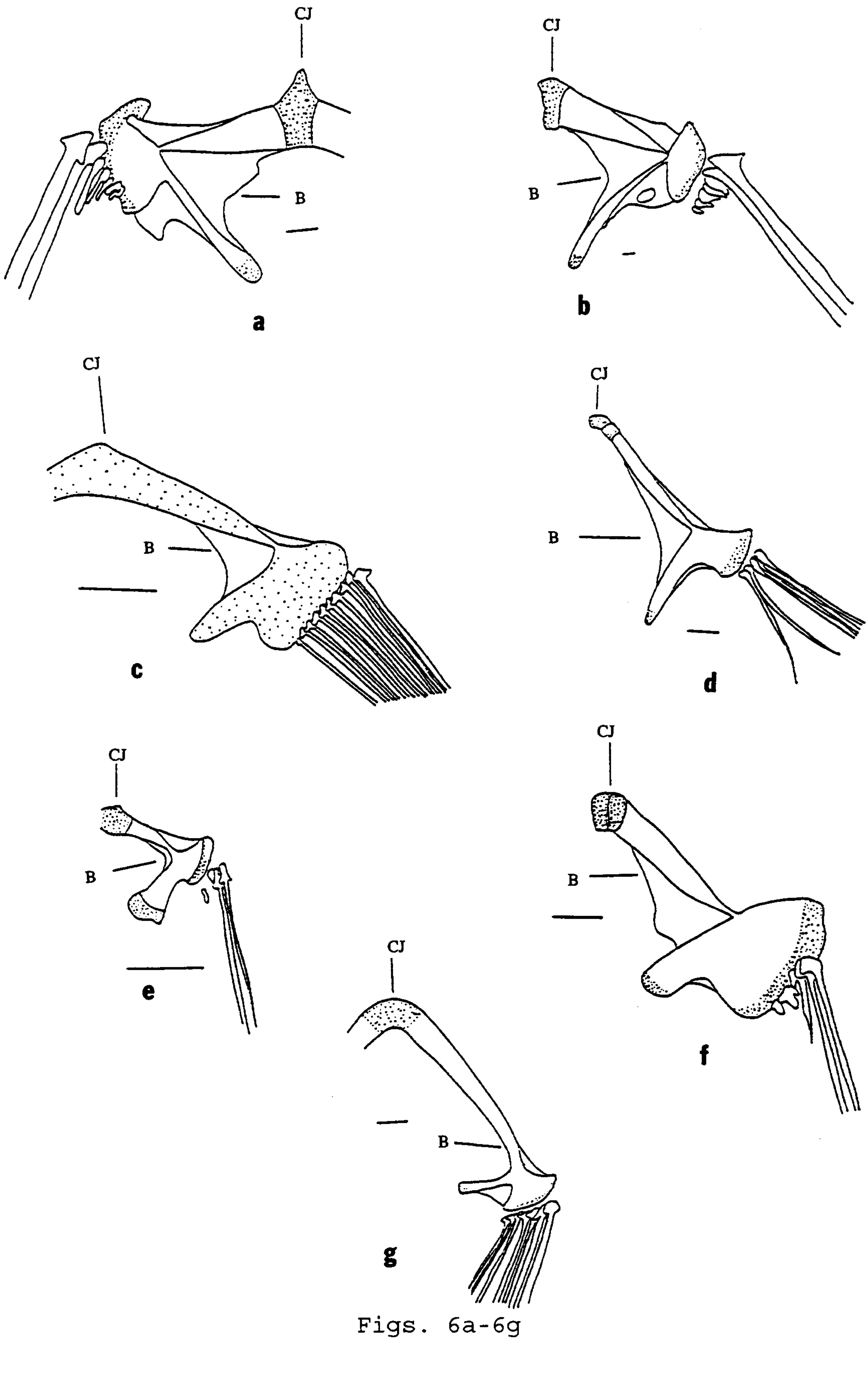
Fig. 6c.- Dorsal view of a half of the pelvic girdle of Laemonema barbatulum juvenile (ARC uncat). Scale = 1 mm

Fig. 6d.- Dorsal view of a half of the pelvic girdle of Guttigadus kongi (MNHNC P. 6589). Scale = 1 mm

Fig. 6e.- Dorsal view of a half of the pelvic girdle of Guttigadus nana (MZUM 214588). Scale = 1 mm

Fig. 6f.- Dorsal view of a half of the pelvic girdle of Guttigadus globiceps (MSU uncat.). Scale = 1 mm

Fig. 6g.- Dorsal view of a half of the pelvic girdle of Physiculus fulvus (USNM 232481). Scale = 1 mm



Figs. 6a-6g

The blade of the inferior arm (**16**) normally lacks a foramen and is considered the plesiomorphic condition because of its absence in outgroups (Fig. 6g and Table 4), state 0 (Fig. 6b, 6c-f), whereas the presence of a foramen on the blade was considered derived (Fig. 6a) state 1 and is present only in L. n.sp. i and L. robustum.

Markle (1989) indicated that gadiform fishes have three pelvic fin-ray ontogenies, one occurs in some morids which have the following ontogeny $N \rightarrow N + n_1 \rightarrow N + n_1 - n_2$, where N is the primordial number of rays first countable, and the n's are subsequent additions or deletions. Adults of most Laemonema have only two visible large pelvic fin rays (**17**) (Fig. 6a-b) and adults of most Guttigadus have three to five visible large pelvic fin rays (Figs. 6d-f). However, cleared and stained adult Laemonema may have one to nine small, inner pelvic rays (Fig. 6c). This evidence, plus the juvenile stage of L. barbatulum discussed below, indicated that there is a reduction in pelvic fin ray size during ontogeny from juvenile to adult. The outgroups had five or more large visible pelvic fin rays, and the outgroup analysis was equivocal (Figs 6g and Table 4). Because outgroups and early ontogenetic stages of the ingroup usually have five or more large visible pelvic fin rays, we polarized the character. A number greater than five was considered plesiomorphic (state 0), and there were two unordered derived states: five to three (state 1), and fewer than three (state 2).

The ratio of the length of the third to the length of the largest pelvic fin ray (**18**) showed three states: more than 40 %, state 0; 15-40%, state 1 (Figs. 6d); and less than 15 %, state 2 (Figs. 6a-b, 6e-f). The outgroup analysis was equivocal (Figs 6g and Table 4).

The total number of all adult pelvic fin rays, including those only seen in cleared and stained specimens (**19**), showed two character states, five or less was state 1 (Figs. 6d-f), and seven or more was state 0 (Figs. 6a-c). The outgroup analysis was equivocal (Figs. 6g and Table 4). The total number of pelvic fin rays ranges from 4-12 in Laemonema, and 3-5 in Guttigadus.

Gas bladder:

The gas bladder of all morids has direct contact with the otic area of the cranium (Figs. 7-8). This characteristic appears to have evolved in many groups of fishes, but in Gadiformes is restricted to morids (Paulin 1988). Paulin (1988) indicated that morids have an anterior and a posterior chamber separated by a constriction (neck) at the level of the parapophyses of the fourth vertebra.

We found variability in constriction presence and length, involving the fourth to the seventh parapophyses. When absent, we can not distinguish whether these species have lost the neck or lost the second chamber and expanded the neck. In spite of this uncertainty regarding homology, we will interpret the structure as loss of the neck. An elongate neck on the gas bladder (**20**) was considered plesiomorphic (state 0, Figs. 7a, 8a-b), because all outgroups had an elongate neck (Figs. 8c-d and Table 4); a small neck was state 1 (Fig 7b), and absence of the neck in L. longipes, L. verecundum and G. nana was state 2 (Figs. 7d-e).

The number of parapophyses (**21**) associated with the posterior chamber was divided into three states. All outgroups had seven or more parapophyses (Figs. 8c-d and Table 4). Thus, we coded seven or more parapophyses as plesiomorphic (state 0, Figs. 7a-b), fewer than seven derived (state 1, Figs. 8a-b), and for those with no posterior chamber there was no possible state (state 9, Fig. 7c-e). The derived state is a synapomorphy for all Guttigadus, except G. nana.

A small patch of ligament on each cornua of the gas bladder and the posterior edges of the cranium (**22**) was either present (state 0, Figs. 7e, 8b) or absent (state 1, Figs. 7a-d, 8a). The outgroup analysis was equivocal (Figs. 8c-d and Table 4). The cornua may be in contact with the skin at each side of the head (**23**) (state 0, Figs. 7a-b, 7e, 8a-b) or not in contact, the derived state 1 (Figs. 7c-d). All outgroups shared the plesiomorphic condition (Figs. 8c-d and Table 4). Two shapes of the cornua (**24**) were found; the cylindrical shape was state 1 (Figs. 7b, 7d-e), and the triangular shape was state 0 (Figs. 7a, 7c, 8a-b). The outgroup analysis was equivocal (Figs. 8c-d and Table 4).

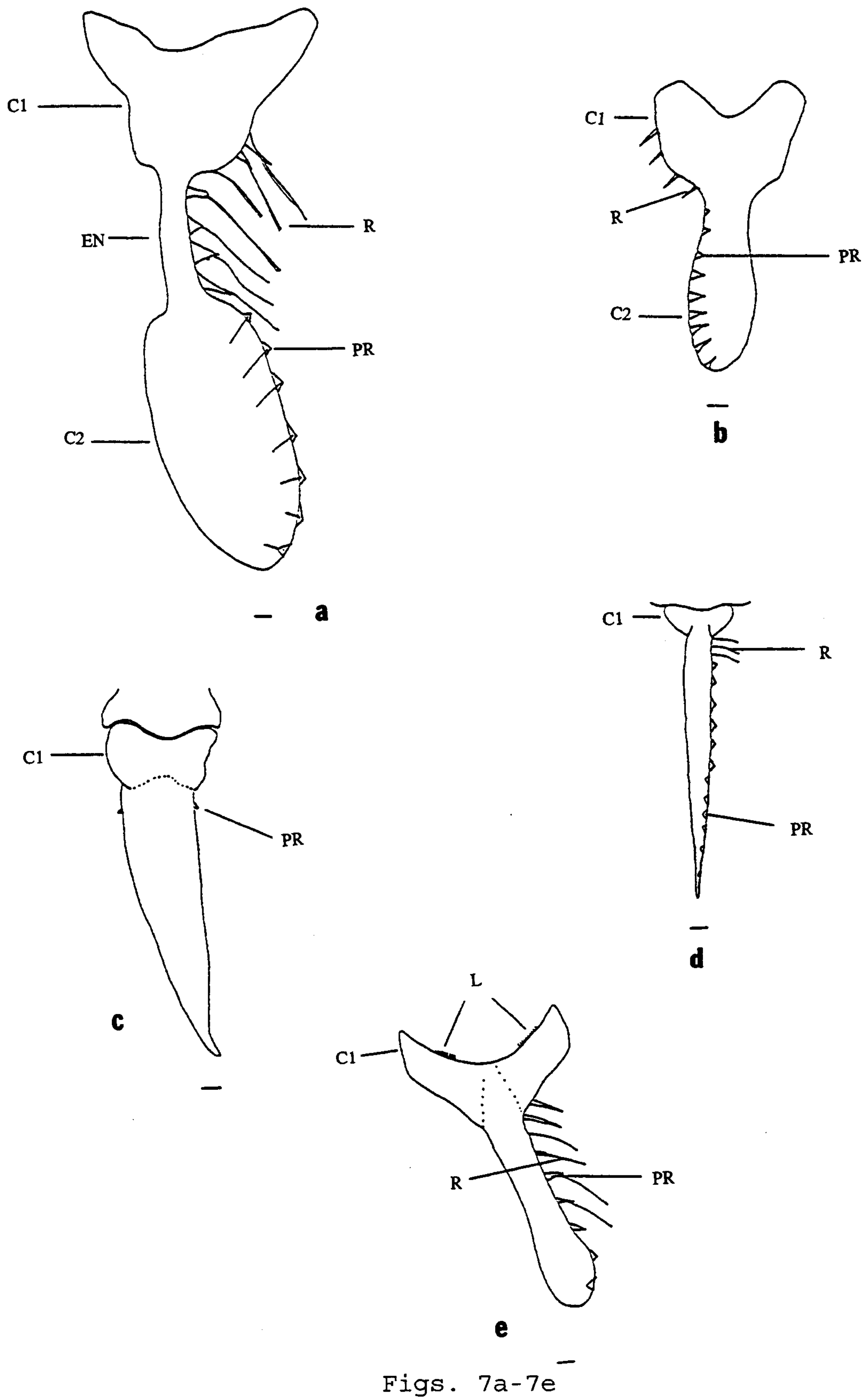
Fig. 7a.- Ventral view of the gas bladder of *Laemonema barbatulum* (UF 13120). Scale = 1 mm

Fig. 7b.- Ventral view of the gas bladder of *Laemonema robustum* (MMF 3128). Scale = 1 cm

Fig. 7c.- Ventral view of the gas bladder of *Laemonema verecundum* (LACM 31118-2). Scale = 1 mm

Fig. 7d.- Ventral view of the gas bladder of *Laemonema longipes* (HUMZ 81033). Scale = 1 cm

Fig. 7e.- Ventral view of the gas bladder of *Guttigadus nana* (ZMUM 214588). Scale = 1 mm



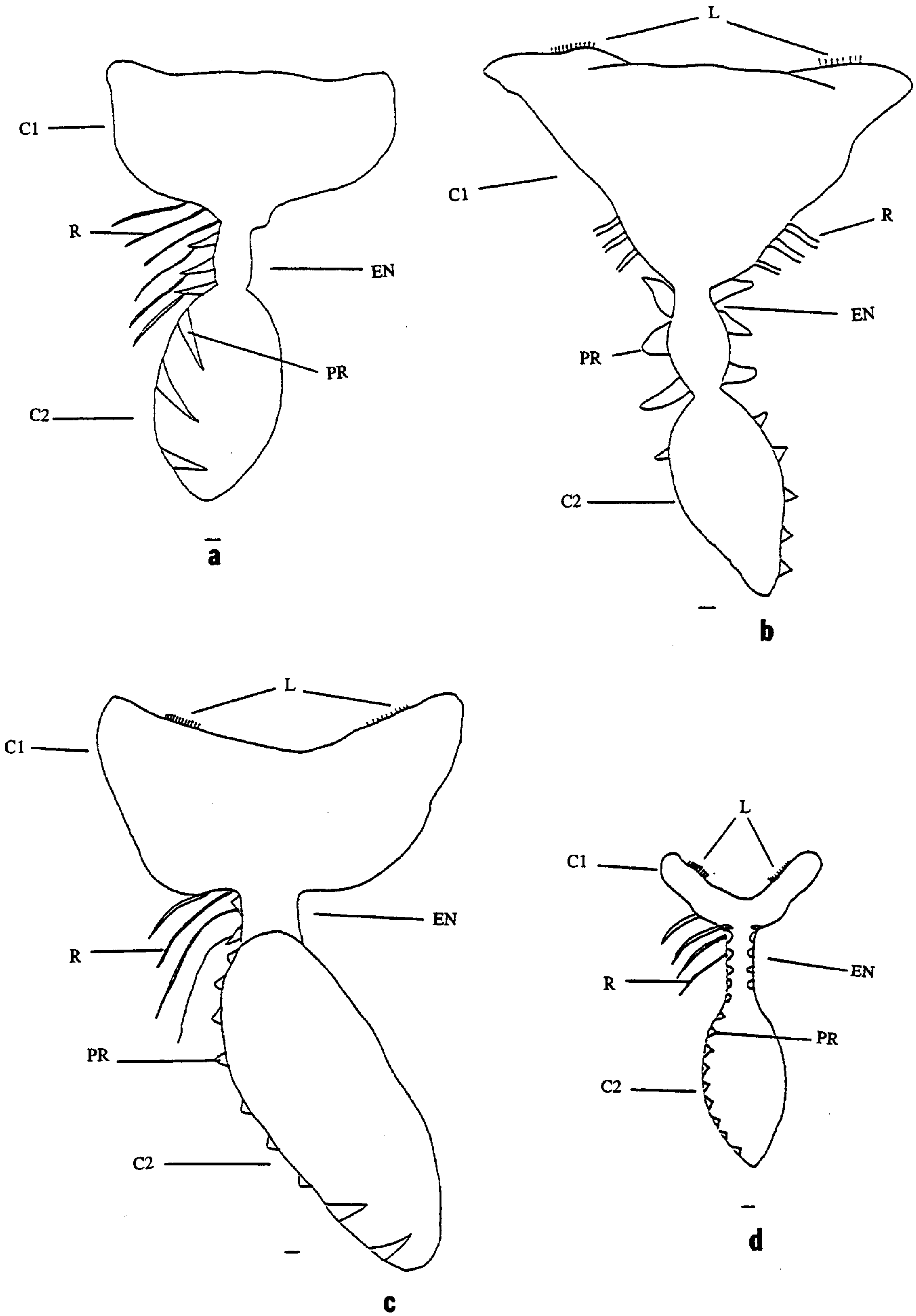
Figs. 7a-7e

Fig. 8a.- Ventral view of the gas bladder of *Guttigadus nudicephalum* (MSU uncat.). Scale = 1 mm

Fig. 8b.- Ventral view of the gas bladder of *Guttigadus latifrons* (MSU uncat.). Scale = 1 mm

Fig. 8c.- Ventral view of the gas bladder of *Physiculus fulvus* (USNM 232481). Scale = 1 mm

Fig. 8d.- Ventral view of the gas bladder of *Lotella fernandeziana* (CAS 24144). Scale = 1 mm



Figs. 8a-8e

Pectoral girdle:

According to Markle (1989) the presence of a foramen located between the scapula and coracoid (Figs. 9a-f), is a derived character in gadiforms. This character can be referred to as either a foramen in both bones (**25**), state 0 (Figs. 9a-b, 9d), or a foramen in the scapula bone, state 1 (Figs. 9c, 9e). The outgroup analysis was equivocal (Fig. 9f and Table 4).

The lower arm of the coracoid (**26**) had two states, long relative to the cleithrum length (state 0, Figs. 9a-c), and short (state 1, Figs. 9d-e). The outgroup analysis was equivocal (Figs. 9f and Table 4). The width of shaft of the lower arm of the coracoid (**27**) either was uniform along its length, state 0 (Figs. 9b-c, 9e), or was wider at its cartilaginous distal tip than near the base of the coracoid plate, state 1 (Figs. 9a, 9d). The outgroup analysis was equivocal (Figs. 9f and Table 4).

Upper jaws and vomer:

In the upper jaw there are multiple rows of teeth (**28**) which may be uniform, minute and caniniform (Figs. 10b-d, 10g), state 0; have an external row of caniniform teeth at least three times the size of inner, minute teeth (Figs. 10a, 10f), state 1; or have an external row of strong caniniform teeth at least five times the size of inner, minute teeth (Fig. 10e), state 2. Outgroup analysis was equivocal (Table 4). The number of teeth on the external row

Fig. 9a.- Medial view of the right pectoral girdle of *Laemonema barbatulum* (UF 13120). Scale = 1 mm

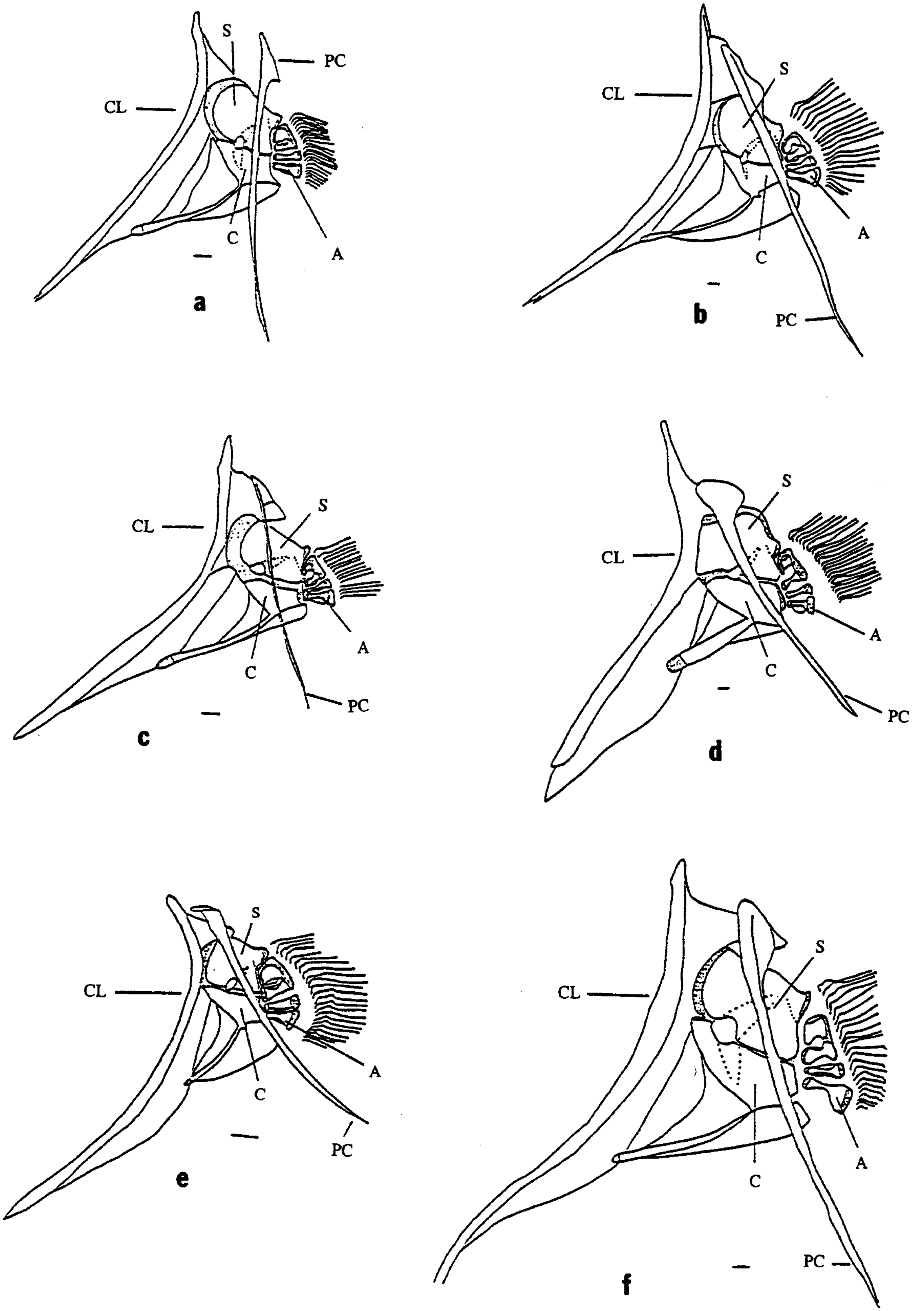
Fig. 9b.- Medial view of the right pectoral girdle of *Laemonema laureysi* (IRSB 175). Scale = 1 mm

Fig. 9c.- Medial view of the right pectoral girdle of *Laemonema longipes* (CAS 47657). Scale = 1 mm

Fig. 9d.- Medial view of the right pectoral girdle of *Guttigadus globosus* (NMNZ 25203). Scale = 1 mm

Fig. 9e.- Medial view of the right pectoral girdle of *Guttigadus nana* (UMMZ 214588). Scale = 1 mm

Fig. 9f.- Medial view of the right pectoral girdle of *Lotella fernandeziana* (CAS 24144). Scale = 1 mm



Figs. 9a-9f

Fig. 10a.- Medial view of the right maxillary of Laemonema barbatulum (UF 13120). Scale = 1 mm

Fig. 10b.- Medial view of the right maxillary of Laemonema longipes (CAS 47657). Scale = 1 mm

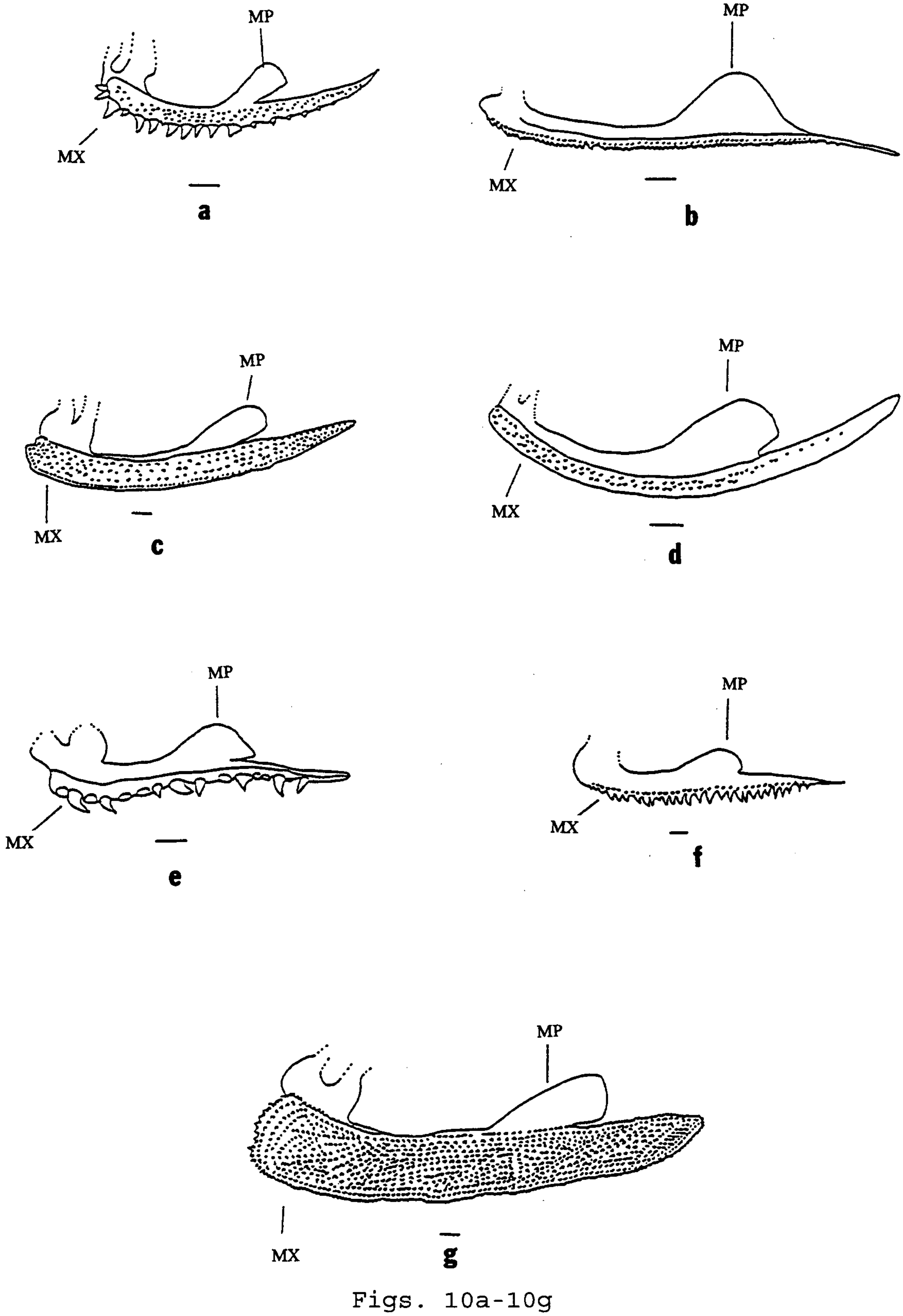
Fig. 10c.- Medial view of the right maxillary of Laemonema rhodochir (PPSIO uncat.). Scale = 1 mm

Fig. 10d.- Medial view of the right maxillary of Guttigadus globosus (NMNZ 25203). Scale = 1 mm

Fig. 10e.- Medial view of the right Maxillary of Guttigadus nudicephalum (MSU uncat.). Scale = 1 mm

Fig. 10f.- Medial view of the right maxillary of Guttigadus kongi (MNHNC P 6589). Scale = 1 mm

Fig. 10g.- Medial view of the right maxillary of Laemonema n.sp. i (RUSI 1423). Scale = 1 mm



Figs. 10a-10g

of one side of the upper jaw (**29**) was more than 50, state 1, or less than 50, state 0. Outgroup analysis was equivocal (Table 4).

The shape of the maxillary process (**30**) was rounded, state 0 (Fig. 10b, 10d-f), or rectangular, state 1 (Fig. 10a, 10c, 10g). The outgroup analysis was equivocal (Table 4). A posterior notch in the maxillary process (**31**) was scored as deep, state 0 (Fig. 10a, 10c, 10g), shallow, state 1 (Fig. 10d-f), or absent, state 2 (Fig. 10b). The outgroup analysis was equivocal (Table 4).

The vomer (**32**) was either absent as in Guttigadus nana, state 0, or present, state 1. The outgroup analysis was equivocal (Table 4). When present, the shape of the vomer (**34**) was either rounded (most species), state 0, or v-shaped as in L. longipes, L. verecundum and G. nudicephalum, state 1. Those species with no vomer were coded as state 9. The outgroup analysis was equivocal (Table 4). The number of teeth on the vomer (**33**) was coded as 0 when there were 10 or fewer, and state 1 when there 11 or more. Again, those species with no vomer were coded as state 9. The outgroup analysis was equivocal (Table 4).

Hyomandibular bone:

A hypothetical hyomandibular bone is showed in Fig. 11a to facilitate the understanding of the following characters related to this bone (Figs. 11-12). A ratio between the total length of the body of the hyomandibular bone and the total length of the opercular arm (**35**) greater than 50.0 % was state 1 (Figs. 11e, 12a-c), and less than 50.0 % was state 0 (Figs. 11b-d, 11f). The outgroup analysis was equivocal (Figs 12d and Table 4). The presence of an antero-lateral blade behind the body of the hyomandibular (**36**) was absent, state 1 in all Guttigadus except G. nana (Figs. 11b-d, 11f, 12c), and present, state 0 in all Laemonema except L. longipes (Figs. 11e, 12a-b). The outgroup analysis was equivocal (Figs. 12d and Table 4). The position of the foramen on the anterior blade of the hyomandibular (**37**) was below the level of the base of the opercular arm (G. nana), state 0 (Figs. 12c), or at the same height as the opercular arm, state 1 (Figs. 11a-f, 12a-b). The outgroup analysis was equivocal (Figs. 12d and Table 4).

The length of the supero-posterior blade of the hyomandibular (**38**) was either short, state 0 (Figs. 11c-f, 12b), or long, state 1 (Figs. 11b, 12a, 12c). The outgroup analysis was equivocal (Figs. 12d and Table 4). The length of the antero-inferior blade of the hyomandibular (**39**) was either short, not reaching the level of the lower articulation of the hyomandibular with the interhyal and symplectic (L. verecundum), state 0 (Fig. 11f) or long, reaching the level of the lower articulation, state 1 (Figs. 11a-e, 12a-c). The outgroup analysis was equivocal (Figs. 12d and Table 4).

Fig. 11a.- Medial view of a hypothetical hyomandibula bone.

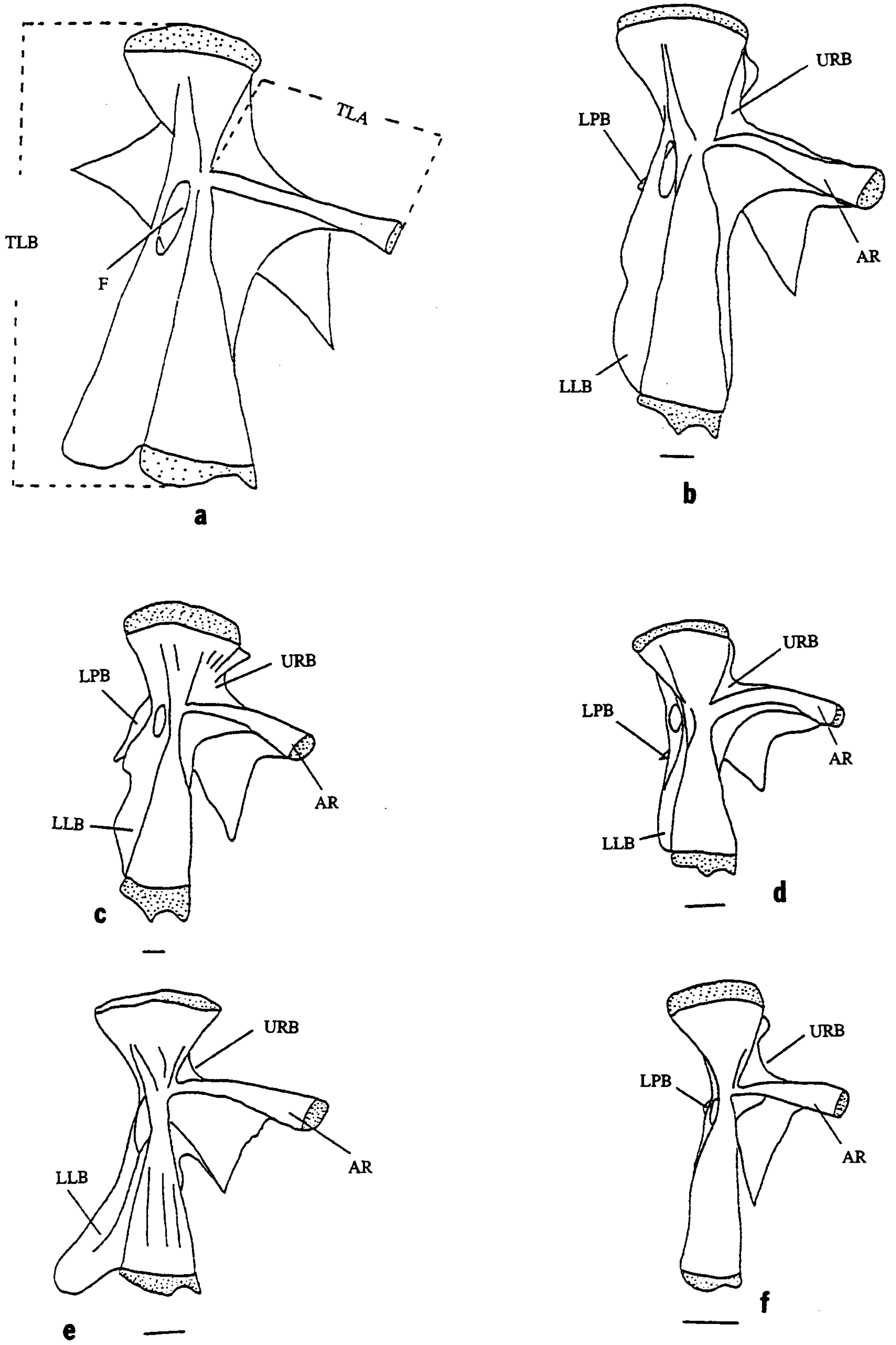
Fig. 11b.- Medial view of the right hyomandibula bone of Laemonema n. sp. g (UF 44476). Scale = 1 mm

Fig. 11c.- Medial view of the right hyomandibula bone of Laemonema gracillipes (USNM 135362). Scale = 1 mm

Fig. 11d.- Medial view of the right hyomandibula bone of Laemonema melanurum (USNM 30441). Scale = 1 mm

Fig. 11e.- Medial view of the right hyomandibula bone of Laemonema longipes (CAS 47657). Scale = 1 mm

Fig. 11f.- Medial view of the right hyomandibula bone of Laemonema verecundum (LACM 31118-2). Scale = 1 mm


TLA
TLB
F
a
URB
LPB
AR
LLB
b
LPB
URB
AR
LLB
c
URB
LPB
AR
LLB
d
URB
AR
LLB
e
URB
LPB
AR
f

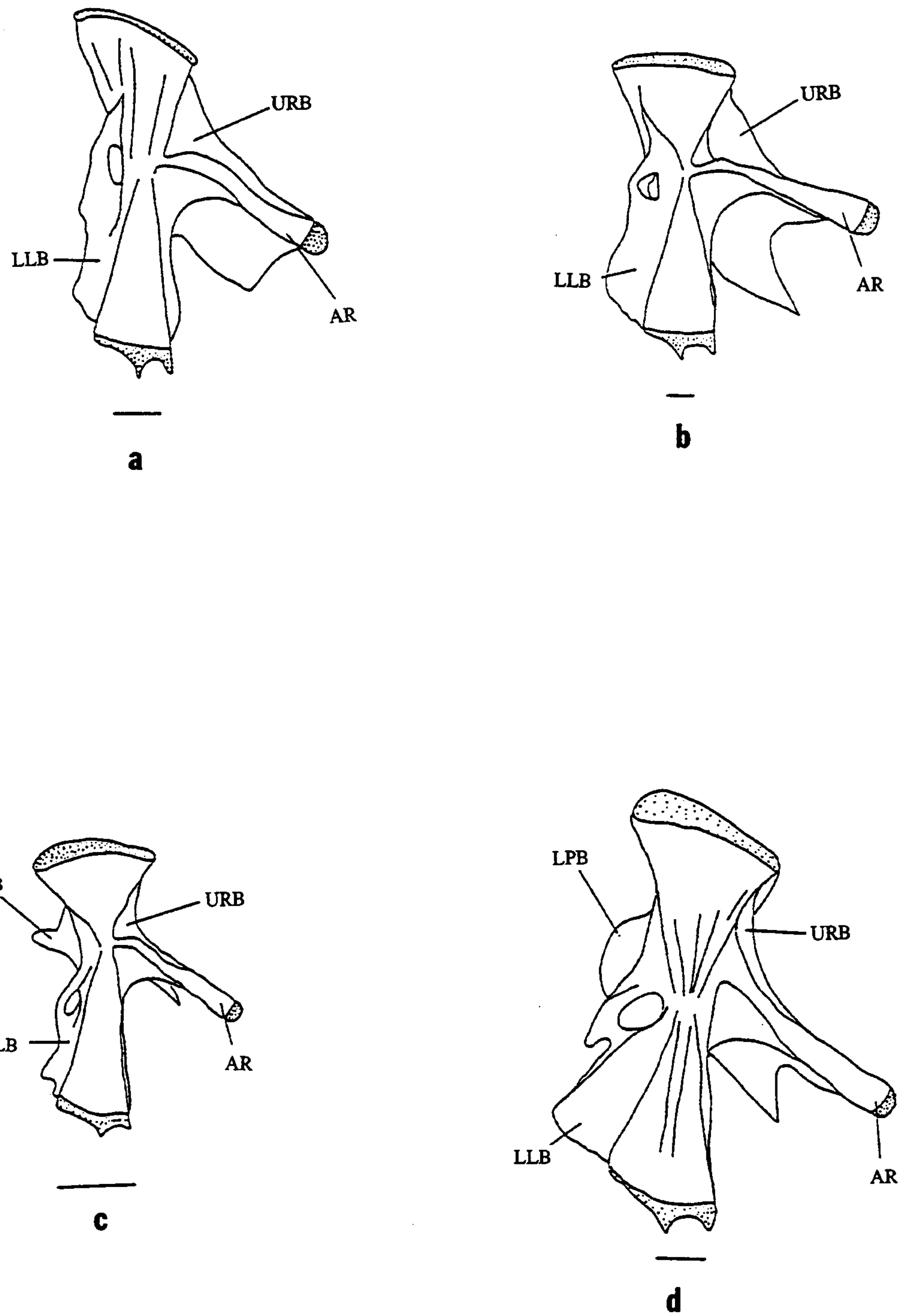
Figs. 11a-11f

Fig. 12a.- Medial view of the right hyomandibula bone of *Guttigadus globiceps* (MSU uncat.). Scale = 1 mm

Fig. 12b.- Medial view of the right hyomandibula bone of *Guttigadus kongi* (MNHNC P 6589). Scale = 1 mm

Fig. 12c.- Medial view of the right hyomandibula bone of *Guttigadus nana* (UMMZ 214588). Scale = 1 mm

Fig. 12d.- Medial view of the right hyomandibula bone of *Physiculus fulvus* (USNM 232481). Scale = 1 mm



Figs. 12a-12d

Caudal skeleton:

The caudal skeleton of gadiform fishes has been well studied (Patterson and Rosen 1989, Markle 1989). The general arrangement for a morid, such as Euclichthys polynemus, is two epurals, a lower autonomous hypural plate of fused hypurals 1 and 2, an upper hypural plate fused to ural centrum 2 composed of fused hypurals 3-5, one parhypural, X and Y bones. Principal or procurrent caudal rays are born on all of these structures; some procurrent rays are unsupported or supported by neural and haemal spines (Figs. 13-15).

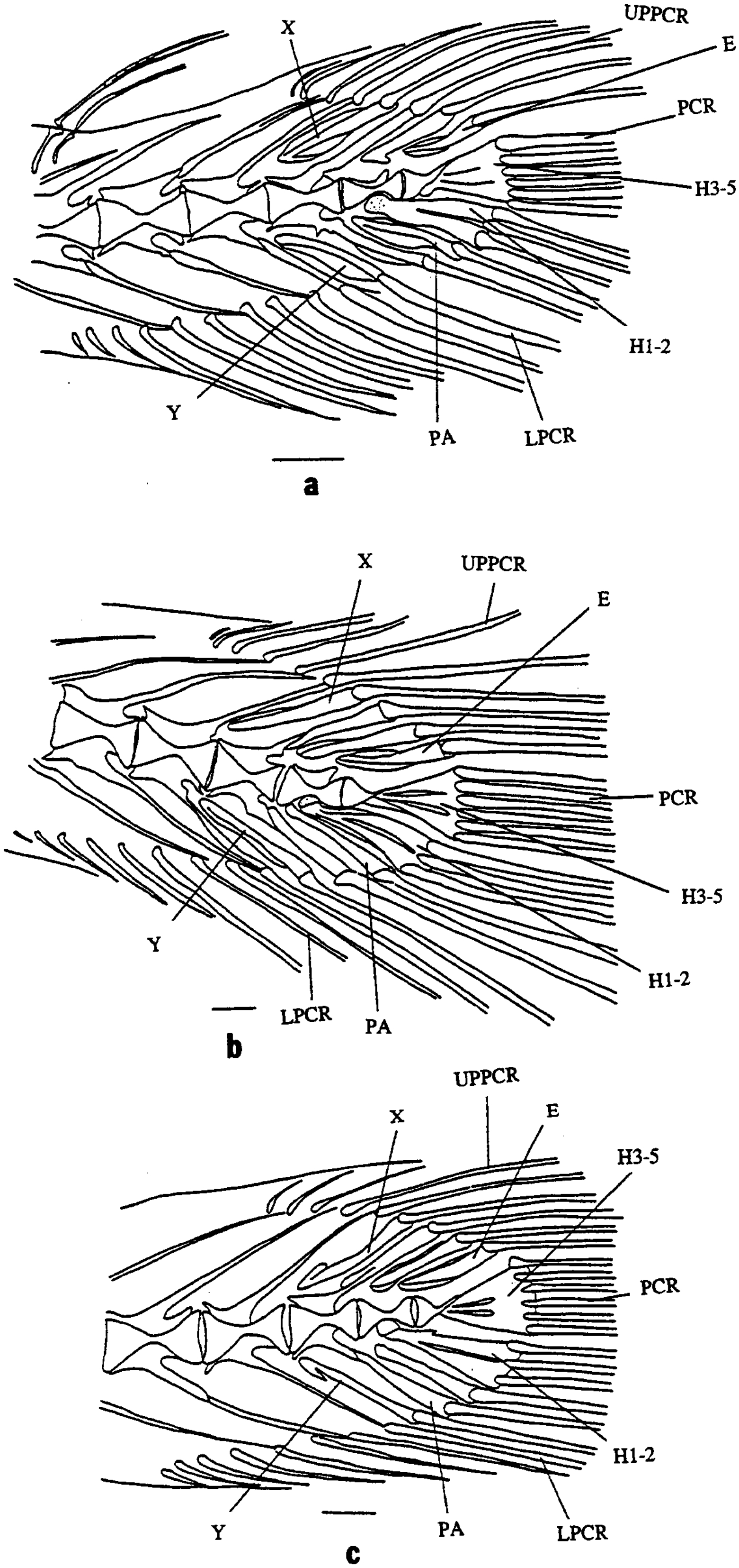
The number of upper procurrent caudal rays (**40**) was 10-14, state 0 (Figs. 13b, 14b, 15a), or 9 or less, state 1 (Figs. 13a, 13c, 14a). The outgroup was equivocal (Figs. 15b and Table 4). The number of lower procurrent caudal rays (**41**), was 16-18 in L. barbatulum, state 0 (Figs. 13a), or 9-15, state 1 (Figs. 13b-c, 14, 15a). The outgroup was equivocal (Figs. 15b and Table 4).

The position of the base of the anterior upper procurrent caudal ray (**42**) opposite the 2nd-4th preural vertebrae was state 0 (Figs. 13b-c, 14b, 15a), and the position opposite the first preural vertebrae was state 1 (Figs. 13a, 14a, 15c). Outgroup analysis was equivocal (Figs. 15b and Table 4). The position of the base of the anterior lower procurrent caudal ray (**43**) opposite the 3rd-5th preural vertebrae was state 0 (Figs. 13a-c, 14b, 15a), and the position opposite the 1st-2nd preural vertebrae was

Fig. 13a.- Caudal skeleton of Laemonema barbatulum (UF 13120). Scale = 1 mm

Fig. 13b.- Caudal skeleton of Laemonema laureysi (IRSB 175). Scale = 1 mm

Fig. 13c.- Caudal skeleton of Laemonema gracillipes (USNM 135362). Scale = 1 mm

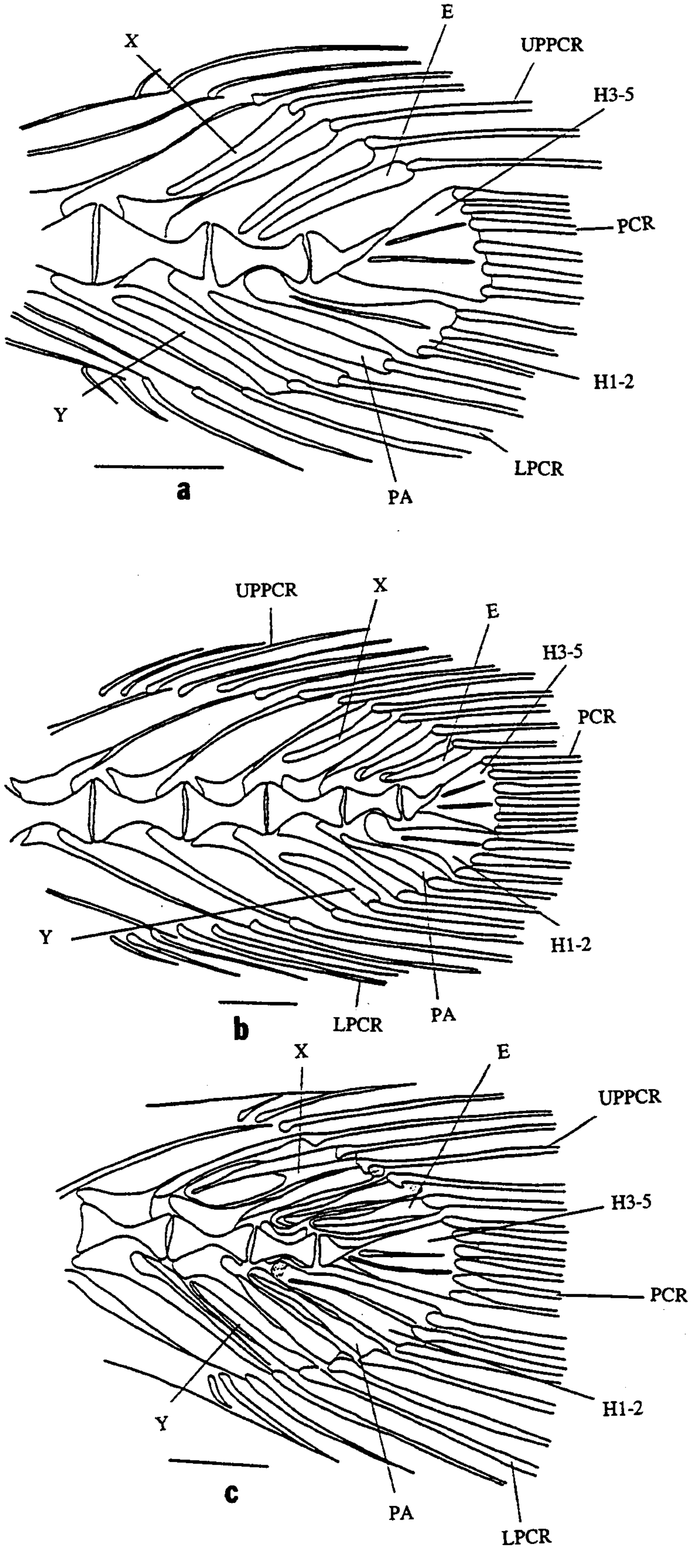

X
UPPCR
E
PCR
H3-5
H1-2
Y
PA
LPCR
a
X
UPPCR
E
PCR
H3-5
Y
H1-2
LPCR
PA
b
UPPCR
X
E
H3-5
PCR
H1-2
Y
PA
LPCR
c

Figs. 13a-13c

Fig. 14a.- Caudal skeleton of _Guttigadus_ _globiceps_ (SAM 12488). Scale = 1 mm

Fig. 14b.- Caudal skeleton of _Guttigadus_ _latifrons_ (IOS 9752#1). Scale = 1 mm

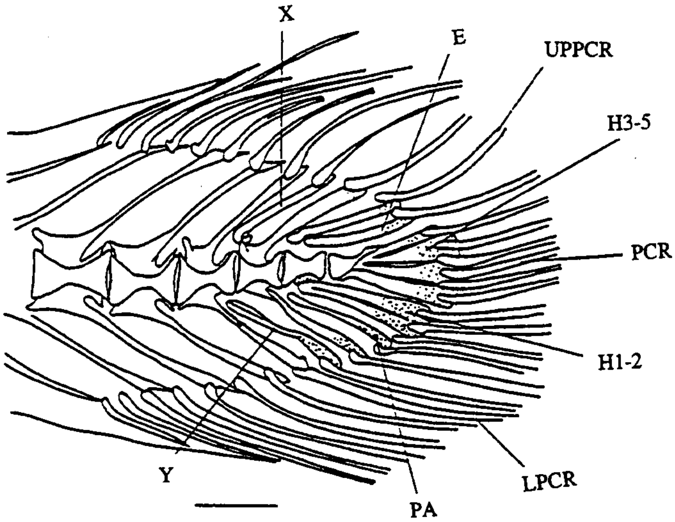
Fig. 14c.- Caudal skeleton of _Guttigadus_ _nana_ (UMMZ 214588). Scale = 1 mm


X
E
UPPCR
H3-5
PCR
H1-2
Y
LPCR
PA
a
UPPCR
X
E
H3-5
PCR
Y
H1-2
LPCR
PA
b
X
E
UPPCR
H3-5
PCR
H1-2
Y
PA
LPCR
c

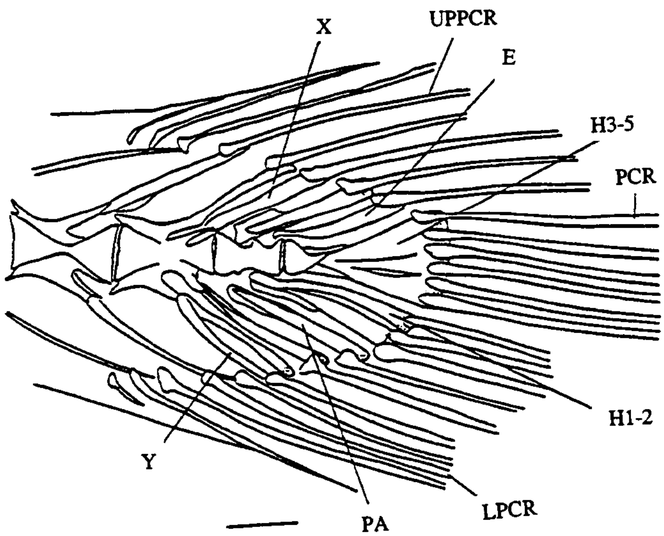
Figs. 14a-14c

Fig. 15a.- Caudal skeleton of _Guttigadus_ _nudicephalum_ (MSU uncat.). Scale = 1 mm

Fig. 15b.- Caudal skeleton of _Physiculus_ _fulvus_ (USNM 232481). Scale = 1 mm



a



b

Figs. 15a-15b

state 1 (Figs. 14a, 14c). Outgroup analysis was equivocal (Figs. 15b and Table 4).

Dorsal and anal fin:

The position of the anus far in front of the anal fin (**44**) was the derived state, state 1, and the position near the anal fin was the plesiomorphic state, state 0. All outgroups have state 0 (Table 4). All Laemonema except L. yuvto have the anus near the anal fin and all Guttigadus except for G. nana have the anus far from the anal fin.

Laminar bone on the first pterygiophore of the first dorsal fin (**45**) was either absent, state 0 (Fig. 16c-d), moderately developed, state 1 (Figs. 16a-b), or well developed, state 2 (Fig. 16e). Outgroup analysis was equivocal (Table 4).

The number of precaudal vertebrae anteriad of the first anal fin ray (**46**) showed two characters states, 14 or greater was state 0, and 13 or less was state 1. The outgroup analysis was equivocal (Table 4). All Guttigadus and some Laemonema had fewer than 13 while most Laemonema 14 or more. Guttigadus nana had only ten precaudal vertebrae anteriad of the first anal fin ray, the lowest value found.

The presence of a fleshy base in the vertical fins (**47**) was derived, state 1, and its absence plesiomorphic, state 0. All outgroups share the plesiomorphic state (Table 4). Laemonema and G. nana have the plesiomorphic state and all

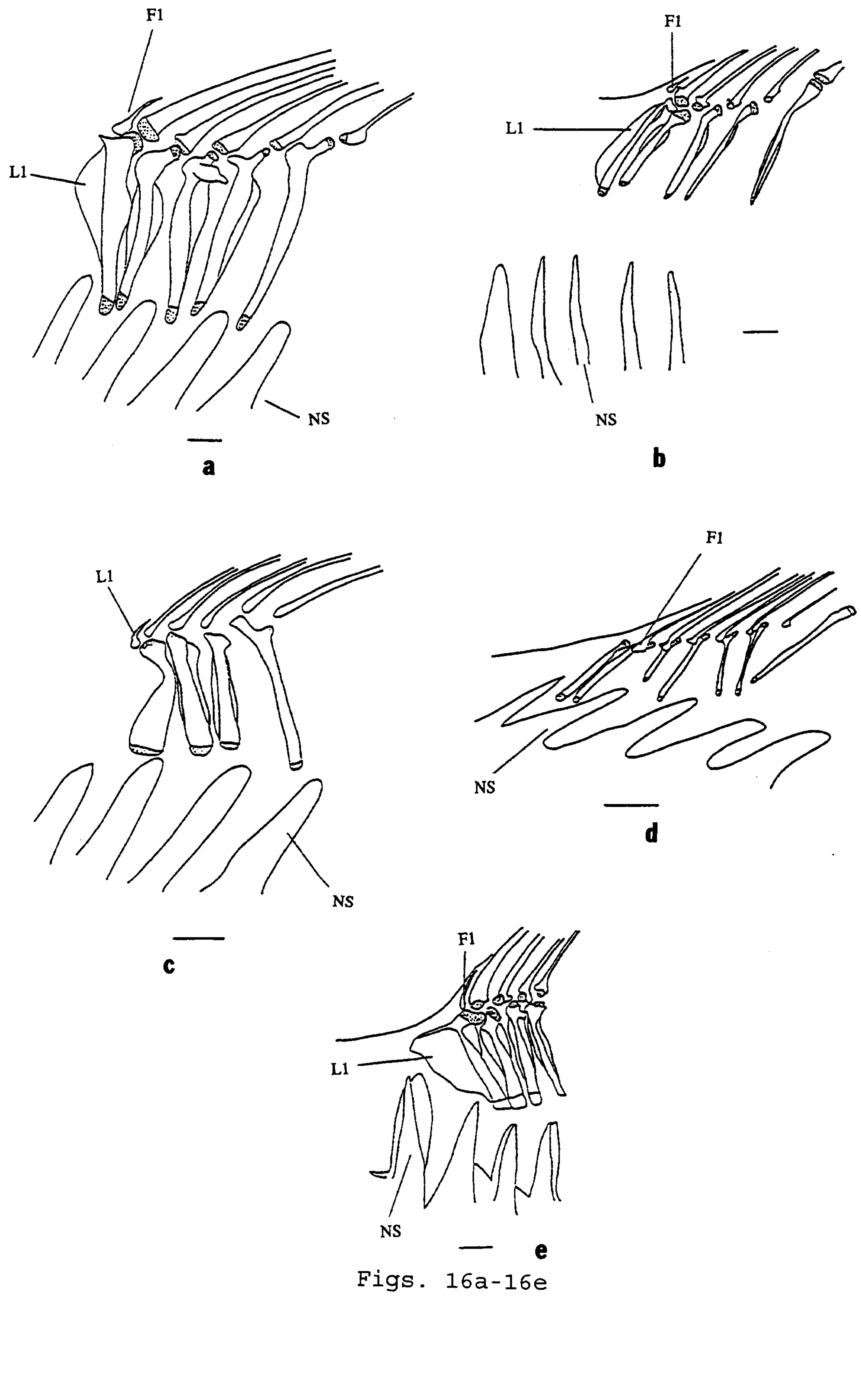
Fig. 16a.- Laminar bone in the first pterygiophore of *Laemonema yarrelli* (MSU 16047). Scale = 1 mm

Fig. 16b.- Laminar bone in the first pterygiophore of *Guttigadus globosus* (NMNZ 25203). Scale = 1 mm

Fig. 16c.- Laminar bone in the first pterygiophore of *Guttigadus latifrons* (MSU uncat.). Scale = 1 mm

Fig. 16d.- Laminar bone in the first pterygiophore of *Guttigadus nana* (UMMZ 214558). Scale = 1 mm

Fig. 16e.- Laminar bone in the first pterygiophore of *Lepidion eques* (USNM 211787). Scale = 1 mm



Figs. 16a-16e

other _Guttigadus_, even juveniles as small as 57 mm (_G_. _kongi_ NMNZ P.23396), have fleshy bases in their vertical fins.

A black stripe along the membranes of the first and second dorsal fins (**48**) was considered derived, state 1, and its absence was plesiomorphic, state 0. All outgroups have the plesiomorphic state (Table 4). The derived state is a synapomorphy of _L_. _barbatulum_ and _L_. _yarrelli_.

Other characters:

Adult living depths (**49**) were coded as state 0 for species living deeper than 70 m and state 1 for _G_. _nana_ which lives shoaler than 70 m. The outgroup analysis was equivocal (Table 4).

Cladograms

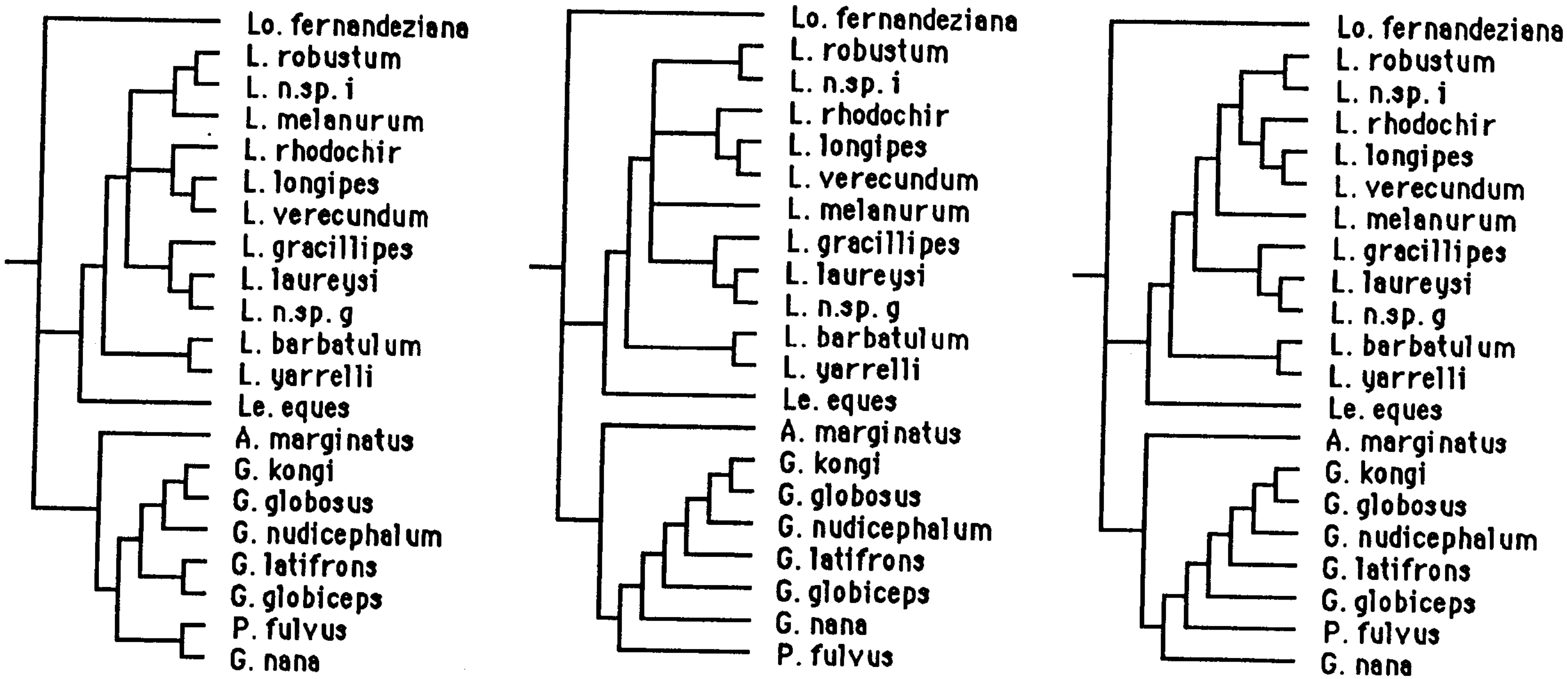
The phylogenetic analysis using all nominal outgroups produced 71 equally parsimonious trees of 149 steps using the heuristic search option in PAUP. The consistency index was 0.389. The low value of the consistency index is because of the large number of homoplasies and the large number of unknown character states in _L_. _yuvto_. Removal of _L_. _yuvto_ from the analysis reduces the number of trees to 12, the number of steps to 147, and increases the CI to 0.395. The 12 trees all suggest that _Laemonema_ _sensu_ _lato_ is not monophyletic but rather contains two clades. One clade includes _Laemonema_ and _Lepidion_; the other includes _Guttigadus_, _Physiculus_, _Austrophycis_, and _Lotella_. Four topologies of three trees each were found within Laemonema. Laemonema melanurum was responsible for the variation in topologies. In the first and second topologies (Figs. 17a and b) L. melanurum appears as a sister species to the clade of L. longipes, L. verecundum, L. rhodochir, L. n.sp. i and L. robustum or in an unresolved trichotomy with this clade and the clade of L. n.sp. g, L. laureysi, and L. gracillipes. In the third and fourth topologies, L. melanurum appears as sister species of the clade of L. n.sp.i plus L. robustum (Figs. 17c and 18) and this clade is fully resolved or part of a trichotomy. In the first and second topologies, L. melanurum must independently acquire a high number of pectoral fin rays (>24). Our preference is to prefer the tree in which the character is acquired once and in which maximum resolution is suggested (Fig. 18) even though support for the resolved tree is based on number of teeth in the maxillary, a character which would seem to be potentially subject to much local selection.

Variation in the topology of the Guttigadus clade involved three basal species. A derived clade of G. globosus, G. kongi, and G. nudicephalum was unchanged in all cladograms (Fig. 17a-c and 18). One outgroup taxon, P. fulvus, was usually the sister to all Guttigadus but sometimes formed a basal sister pair with G. nana or was the second branch within Guttigadus after a basal G. nana. All other variation involved G. globiceps and G. latifrons which either formed a pair that was the sister group to the

Fig. 17 a. Topology of Laemonema and Guttigadus species using four outgroups (Austrophycis marginatus, Lepidion eques, Lotella fernandeziana and Physiculus fulvus).

Fig. 17 b. Topology of Laemonema and Guttigadus species using four outgroups (Austrophycis marginatus, Lepidion eques, Lotella fernandeziana and Physiculus fulvus).

Fig. 17 c. Topology of Laemonema and Guttigadus species using four outgroups (Austrophycis marginatus, Lepidion eques, Lotella fernandeziana and Physiculus fulvus).



Lo. fernandeziana
L. robustum
L. n.sp. i
L. melanurum
L. rhodochir
L. longipes
L. verecundum
L. gracillipes
L. laureysi
L. n.sp. g
L. barbatulum
L. yarrelli
Le. eques
A. marginatus
G. kongi
G. globosus
G. nudicephalum
G. latifrons
G. globiceps
P. fulvus
G. nana
Lo. fernandeziana
L. robustum
L. n.sp. i
L. rhodochir
L. longipes
L. verecundum
L. melanurum
L. gracillipes
L. laureysi
L. n.sp. g
L. barbatulum
L. yarrelli
Le. eques
A. marginatus
G. kongi
G. globosus
G. nudicephalum
G. latifrons
G. globiceps
G. nana
P. fulvus
Lo. fernandeziana
L. robustum
L. n.sp. i
L. rhodochir
L. longipes
L. verecundum
L. melanurum
L. gracillipes
L. laureysi
L. n.sp. g
L. barbatulum
L. yarrelli
Le. eques
A. marginatus
G. kongi
G. globosus
G. nudicephalum
G. latifrons
G. globiceps
P. fulvus
G. nana

Fig. 17 a-c.

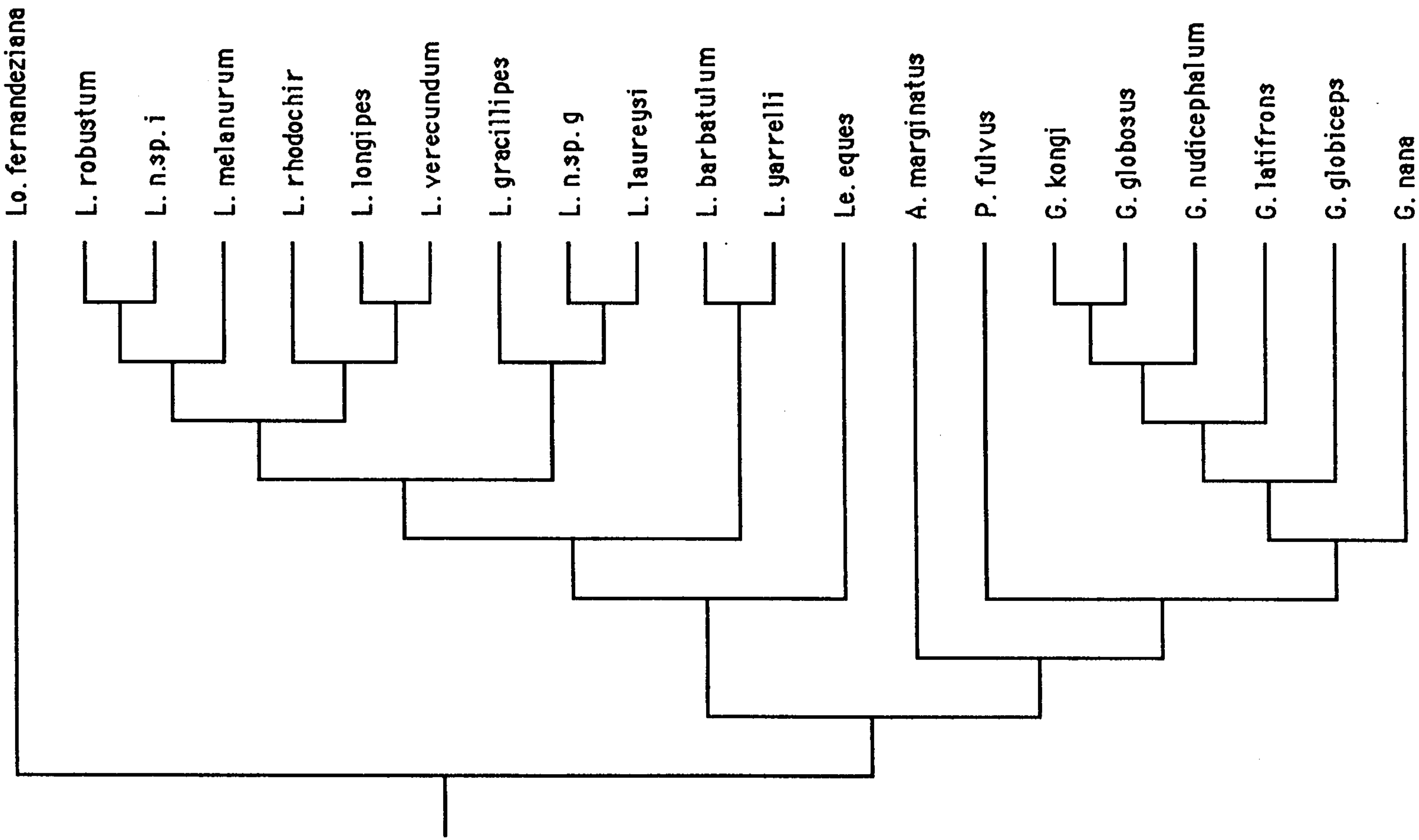


Fig. 18. Relationship cladogram of Laemonema sensu lato with four outgroups (A. marginatus, Le. eques, Lo. fernandeziana and P. fulvus) (CI=0.395, length=147).

derived clade or did not form a pair and _G_. _globiceps_ was basal (Fig. 18). At least in terms of overall appearance, _G_. _latifrons_ is almost indistinguishable from members of the derived clade (Markle and Meléndez 1988) whereas _G_. _globiceps_ is readily diagnosable from this group. The cladogram in Fig. 18 thus represents our best estimate of _Guttigadus_ phylogeny when using multiple outgroups.

Because we are uncertain of sister group relationships, we attempted to increase resolution within _Laemonema_ _sensu_ _lato_ by using each outgroup taxon (_Austrophycis_ _marginatus_, _Lepidion_ _eques_, _Lotella_ _fernandeziana_, and _Physiculus_ _fulvus_) singly. Two sister clades, _Laemonema_ and _Guttigadus_ were in each of the various parsimonious trees for each outgroup. Because Paulin (1989) included the "_Laemonema_" subgroup in his "_Physiculus_" group and we have two additional synapomorphies for _Physiculus_ + _Laemonema_ _sensu_ _lato_ (**39** - long antero-inferior blade of the hyomandibular, and **41** - low number (9-15) of lower procurrent caudal rays), we selected _P_. _fulvus_ as the most likely sister taxon and best possible outgroup taxon. Twenty-two most parsimonious trees were obtained using the branch and bound option in PAUP (CI= 0.483, length= 118). The _Guttigadus_ clade was exactly the same in each of the twenty-two trees and had the topology shown in Fig. 19. The _Laemonema_ clade had more topologies but two that differed primarily in their basal species. One topology had a basal clade made up of the sister species _L_. _longipes_ and _L_. _verecundum_ (Fig. 19a) and

Fig. 19 a. Example of a topology with Laemonema longipes and Laemonema verecundum as a basal species for the Laemonema clade with Physiculus fulvus as an outgroup.

Fig. 19 b. Example of a topology with Laemonema n.sp. g as a basal species for the Laemonema clade with Physiculus fulvus as an outgroup.

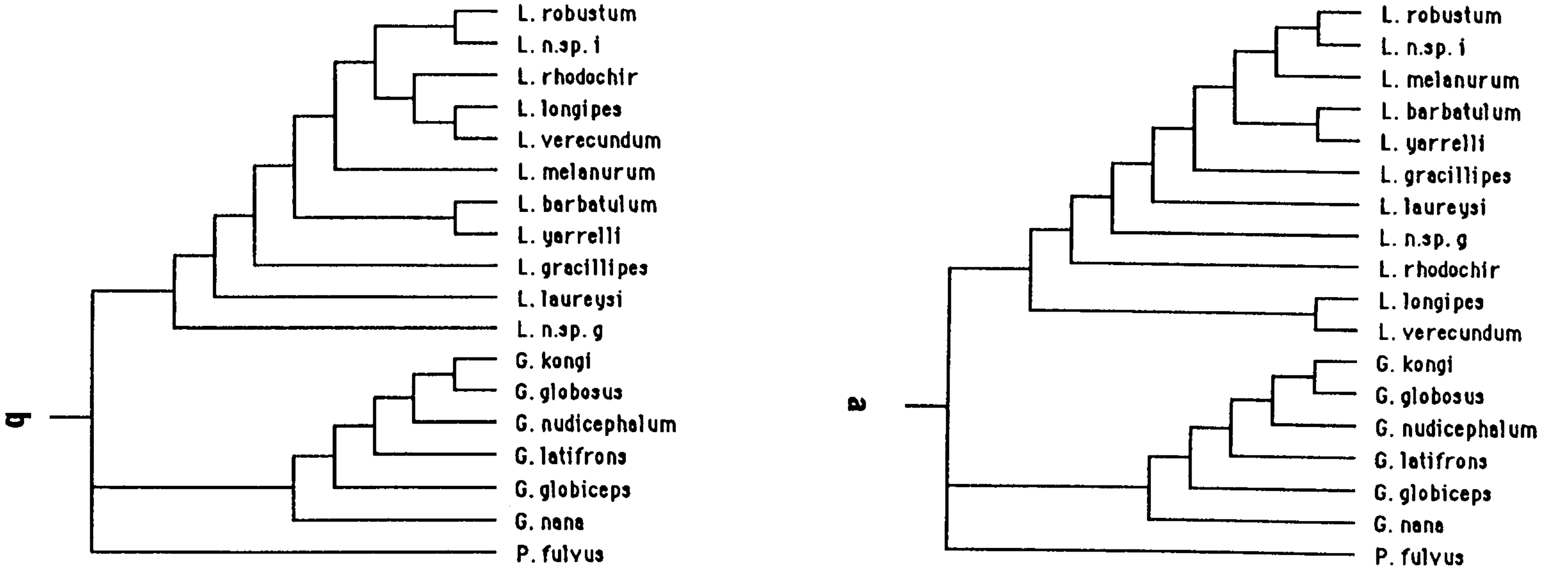

b
L. robustum
L. n.sp. i
L. rhodochir
L. longipes
L. verecundum
L. melanurum
L. barbatulum
L. yarrelli
L. gracillipes
L. laureysi
L. n.sp. g
G. kongi
G. globosus
G. nudicephalum
G. latifrons
G. globiceps
G. nana
P. fulvus
a
L. robustum
L. n.sp. i
L. melanurum
L. barbatulum
L. yarrelli
L. gracillipes
L. laureysi
L. n.sp. g
L. rhodochir
L. longipes
L. verecundum
G. kongi
G. globosus
G. nudicephalum
G. latifrons
G. globiceps
G. nana
P. fulvus

Fig. 19 a - b.

the other had a basal L. n.sp. g with the L. longipes + L. verecundum pair in a derived clade with L. rhodochir (Fig. 19b). There are few reasons to choose one topology over the other. When the L. longipes + L. verecundum pair is basal, there is a synapomorphy for the other species of Laemonema (the triangular shape of the maxillary process - **30**) whereas the alternative phylogeny relies on homoplasies. Twelves trees contain this topology, four of which contain polytomies. Seven of the eight fully resolved trees place L. rhodochir as the next branch. In the previous analysis L. rhodochir was also only one node removed from L. longipes + L. verecundum (Fig. 18). A derived clade of L. melanurum and L. n.sp. i plus L. robustum was found in 7 of the 8 trees (Fig. 19a) with the alternative tree requiring independent acquisition of a high number of pectoral fin rays. When these seven trees are compared to the topology in Fig. 18, only one retains most 2 and 3 species terminal clades (Fig. 20). This topology, though tentative at best, represents our best current view of relationships and has some intuitive appeal to us. The tentative position of L. yuvto in a polytomy with L. melanurum, L. robustum and L. n.sp. i, is based solely on the large number of pectoral fin rays.

Monophyly of the ingroup, Laemonema sensu lato, is supported at node A (Fig. 20) by one synapomorphy, the length of the third pelvic fin ray being less than 45% the length of the longest pelvic fin ray (**18**). This is

Fig. 20.- Cladogram of hypothesized relationship of genera _Laemonema_ and _Guttigadus_ species with _P_. _fulvus_ as an outgroup (CI=0.483, length=118). Characters at nodes A-M: Synapomorphies: A) 18, B1) 23,31 C) 30 D1) 48 G) 3 H) 13,16,20 I) 2,26 J) 1,21,47 K) 18. Homoplasies: A) 4,32,37 B) 10,12,14,17,18, 22,30,38,43,46, B1) 20,34 C) 46 C1) 8,27 D) 28,43 D1) 35 E) 42 F) 11,31 F2) 8,33 G) 27 G1) 25 H) 20,24 I) 9,11,19,35,45 I1) 15,20,24,25 J) 5,36,44 J1) 12 K) 40,42,43 K1) 9,25 L) 15,45 L1) 3,22,33,34 M) 11,38. Reversals: B1) 17 I1) 4,32,37. Numerals refers character state in the text.

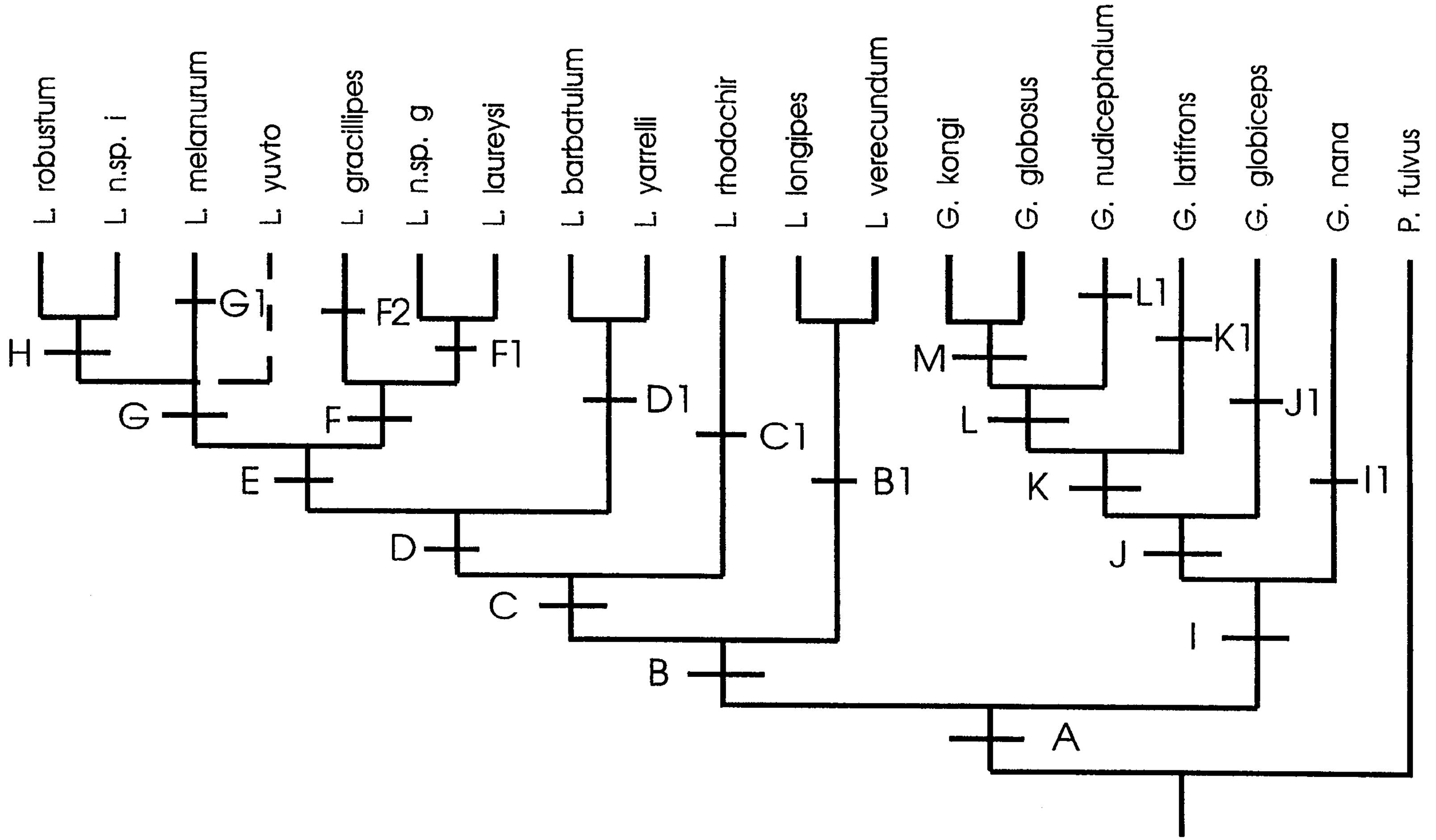

L. robustum
L. n.sp. i
L. melanurum
L. yuvto
L. gracilipes
L. n.sp. g
L. laureysi
L. barbatulum
L. yarrelli
L. rhodochir
L. longipes
L. verecundum
G. kongi
G. globosus
G. nudicephalum
G. latifrons
G. globiceps
G. nana
P. fulvus
G1
F2
F1
H
G
F
D1
C1
B1
E
D
C
B
A
M
L1
K1
L
J1
K
I1
J
I

Fig. 20.

essentially the traditional character, often described as two long pelvic rays, used to define the group. Homoplasies supporting this node are: more than eight lower gill rakers (**4**), with a reversal in G. nana; the presence of a vomer (**32**), with a reversal in G. nana; and the position of the foramen at the same height of the opercular arm in the hyomandibular bone (**37**), with a reversal in G. nana.

We recognize two genera, Laemonema and Guttigadus, because the clades were consistently identified in all of the phylogenetic analyses. However, Laemonema is most sensitive to outgroup selection, and using P. fulvus, the monophyly of Laemonema (node B, Fig. 20) is only weakly supported by 10 homoplasies: presence of an interarcual cartilage (**10**, independently acquired in G. globosus); first epibranchial 90-120% of length of second epibranchial (**12**, less than 90% in L. robustum and independently elongated in G. globiceps and G. kongi); pointed joining cartilage of superior arm of pelvic girdle (**14**), independently acquired in G. nana; only two pelvic rays visible (**17**), with reversal to next state in L. verecundum (4 rays); length of third pelvic fin ray (**18**) less than 15%, independently acquired in G. nana and G. globiceps, absence of ligament between gas bladder and cranium (**22**, independently lost in G. nudicephalum); rectangular shape of maxillary process (**30**, rounded in L. longipes and L. verecundum); short supero-posterior blade of hyomandibular (**38**, multi-homoplastic); base of anterior lower procurrent caudal fin opposite 3rd to

5th preural vertebrae (**43**, multi-homoplastic); and 14 or more precaudal vertebra anteriad of first anal fin ray (**46**, four species have less than 13).

Node B1 supports the sister species Laemonema longipes and L. verecundum (Fig. 20) with two synapomorphies and two homoplasies. The synapomorphies are the cornua that do not reach the skin in the area above the operculum (**23**), and the absence of a posterior notch in the base of the maxillary process (**31**). The homoplasies are the absence of a neck between chambers in the gas bladder (**20**), and the v-shaped vomer (**34**). Laemonema longipes is supported by seven homoplasies; small size of the second pharyngobranchial (**7**); absence of the uncinate process (**9**); angle equal or greater than 90° between superior and inferior arms on each side of the pelvic girdle (**15**); cylindric type of cornua of the gas bladder (**24**); foramen only in the scapula bone (**25**); ratio between the length of the hyomandibular bone and the length of its opercular arm greater than 50% (**35**); and absence of the antero-lateral blade behind the body of the hyomandibular (**36**). Laemonema verecundum is supported by four homoplasies; more than two visible pelvic fin rays (a reversal **17**); wider cartilaginous distal tip than near the base of the coracoid plate (**27**); short antero-inferior blade of the hyomandibular bone (**39**); and 10 to 14 upper procurrent caudal fin rays (**40**).

Node C (Fig. 20) is supported by one synapomorphy and one homoplasy. The synapomorphy is the rectangular shape of the maxillary process (**30**). The homoplasy is more than 13 precaudal vertebrae anterior to the first anal fin ray (**46**). Node C1 support L. rhodochir with two homoplasies; two articulations on pharyngobranchial 2 (**8**); and wider cartilaginous distal tip of the coracoid plate (**27**).

Node D (Fig. 20) is supported by two homoplasies; uniform, minute, and caniniform teeth in the upper jaw (**28**); and base of the anterior lower procurrent caudal ray opposite to the 3rd-5th preural vertebrae (**43**). Node D1 supports the sister species Laemonema barbatulum and L. yarrelli with one synapomorphy and one homoplasy (Fig. 20). The synapomorphy is the presence of a black stripe in the upper portion of the first and second dorsal fin (**48**). The homoplasy is that the length of the hyomandibular is greater than 50% of its opercular arm (**35**). Laemonema barbatulum is supported by one autapomorphy, the high number of lower procurrent caudal rays (**41**), and four homoplasies, the different width of the cartilaginous tip of the coracoid plate (**27**), the presence of one external row of caniniform teeth at least three times the size of the minute teeth on inner rows (**28**), the large supero-posterior blade of the hyomandibular (**38**), and 13 or fewer precaudal vertebrae anteriad of the first anal fin ray (**46**). Laemonema yarrelli is supported by one homoplasy, the equal width of the shaft of the coracoid plate (**27**).

Node E (Fig. 20) is supported by one homoplasy the position of the anterior upper procurrent caudal ray opposite the 2nd-4th preural vertebrae (**42**). This node E supports the nodes F and G (Fig. 20)

Node F (Fig. 20) is supported by two homoplasies, the absence of the interarcual ligament (**11**), and a shallow notch in the maxillary process (**31**). Laemonema gracillipes is supported at node F2 by two homoplasies, the presence of two articulations in pharyngobranchial 2 (**8**), and, more than 11 teeth on vomer (**33**). Node F1 support L. n. sp. g and L. laureysi. Laemonema laureysi is supported by one homoplasy, ten or more upper procurrent caudal fin rays (**40**). Laemonema n.sp. g, is supported by two homoplasies, the greater length of the supero-posterior blade of the hyomandibular (**38**), and the base of the anterior upper procurrent caudal ray opposite the 2nd-4th preural vertebrae (**42**).

Node G is supported by one synapomorphy, more than 24 pectoral fin rays (**3**) and one homoplasy the uniform width of the shaft of the coracoid plate (**27**). This node G support also a polytomy. The polytomy include Laemonema melanurum at node G1 supported by one homoplasy the presence of a foramen only in the scapula bone (**25**). The sister species L. robustum and L. n. sp. i are also included in the polytomy at node H (Fig. 20), and supported by three synapomorphies: presence of a groove on the 3rd and 4th strut of the 3rd pharyngobranchial (**13**); presence of a foramen in the pelvic girdle (**16**); and presence of a small neck in the swim bladder (**20**). Two homoplasies also support the sister species, the cylindrical shape of the cornua (**24**), and more than 50 teeth on the external row of one side of the upper jaws (**29**). Laemonema robustum is supported by five homoplasies: presence of two articulation on pharyngobranchial 2 (**8**); length of the first epibranchial less than 90% the second epibranchial (**12**); more than 10 teeth on vomer (**33**); hyomandibular bone greater than 50% the length of the opercular arm (**35**); and 10-14 upper procurrent caudal rays (**40**). Laemonema n. sp. i is supported by five homoplasies: absence of interarcual ligament (**11**); a long supero-posterior blade of the hyomandibular (**38**); position of the base of the anterior upper procurrent caudal ray opposite the first preural vertebrae (**42**); absence of the laminar bone on the first pterygiophore of the first dorsal fin (**45**); and less than 14 precaudal vertebrae anterior to the first anal ray (**46**). We included Laemonema yuvto in forming the polytomy because it has more than 24 rays in the pectoral fin (**3**).

Guttigadus is supported by two synapomorphies at node I (Fig. 20), the PCA score of D2, A, PCV and CV (**2**), and the comparatively short length of the coracoid arm in the pectoral girdle (**26**). Five homoplasies also support this clade: absence of the uncinate process on the first epibranchial (**9**) with a reversal in G. latifrons, and independently lost in L. longipes; absence of the interarcual ligament (**11**) with a reversal in G. globosus and G. kongi; five or fewer pelvic fin rays in adults (**19**) independently acquired in L. longipes and L. verecundum; a hyomandibular more than 50% longer than its opercular arm (**35**), independently elongated in L. barbatulum, L. longipes, L. robustum and L. yarrelli; and absence of laminar bone on the first pterygiophore of the first dorsal fin (**45**), with reversals in G. globosus, G. kongi, and G. nudicephalum.

Guttigadus nana (Fig. 20) is supported at node I1 by two autapomorphies, the absence of pharyngobranchial 2 (**7**), and a living depth less than 80 m (**49**); and four homoplasies, an angle equal or greater than 90° between arms on each side of pelvic girdle (**15**), the absence of a neck between gas bladder chambers (**20**), a cylindric type of cornua of the gas bladder (**24**), and a foramen in the scapula bone only (**25**).

All other Guttigadus are supported by three synapomorphies and three homoplasies at node J (Fig. 20). The synapomorphies are: wide (7.1-15 % SL) interorbital width (**1**), fewer than seven parapophyses associated with the second chamber of the gas bladder (**21**), and fleshy base of the vertical fins (**47**). Three homoplasies are: highly modified scales on the lateral line (**5**), independently acquired in L. yuvto, absence of an anterior lateral blade behind the body of the hyomandibular (**36**), independently acquired in L. longipes, and the far position of anus related to the beginning of the anal fin (**44**), independently acquired in L. yuvto.

Guttigadus globiceps (Fig. 20) is supported at node J1 by one autapomorphy, more than 21 lower gill rakers (**4**), and one homoplasy, the first epibranchial is 90-120 % the length of the second epibranchial (**12**).

The node K (Fig. 20) is supported by one synapomorphy, the third pelvic fin ray is 15-40 % the length of the largest pelvic fin rays (**18**), and three homoplasies: 10-14 upper procurrent caudal fin rays (**40**), the first preural vertebrae opposite the base of the most anteriad upper procurrent caudal fin ray (**42**), and the 3rd to 5th preural vertebrae opposite most anteriad ray of the lower procurrent caudal ray (**43**).

Guttigadus latifrons is supported at node K1 by two homoplasies, the presence of an uncinate process in the first epibranchial (**9**), and a foramen only in the scapula bone of the pectoral girdle (**25**).

Node L (Fig. 20) is supported by two homoplasies, an angle equal to or greater than 90° between superior and inferior pelvic arms (**15**), and the presence of a medium size laminar bone on the first pterygiophore of the first dorsal fin (**45**). Guttigadus nudicephalum is supported at node L1 by one autapomorphy, the teeth in the upper jaws at least five times the size of the minute teeth (**28**), and four homoplasies: more than 25 pectoral fin rays (**3**), presence of a small patch of ligament on each cornua of the gas bladder (**22**), more than 10 teeth on the vomer (**33**), and triangular or v-shaped vomer (**34**).

The sister species G. globosus and G. kongi are supported at node M (Fig. 20) by two homoplasies, the presence of an interarcual ligament (**11**), and the presence of a short supero-posterior blade of the hyomandibular bone (**38**). Guttigadus globosus is supported by one homoplasy, the presence of an interarcual cartilage (**10**). Guttigadus kongi is supported by two homoplasies, first epibranchial 90-120% of the second epibranchial (**12**), and teeth on the upper jaws three times larger than the inner teeth (**28**).

The results of this cladogram (Fig. 20) agree with Rass's (1954) general idea of interrelationship of Laemonema sensu lato. Rass (1954) distinguished two natural groups, equivalent to Laemonema and Guttigadus as recognized here. In fact, one of his characters, the wide interorbital width, is a synapomorphy of all Guttigadus, except G. nana, and is one of the most easily recognized feature of the genus. Guttigadus, as defined herein, includes four species removed from Laemonema (G. globiceps, G. kongi, G. latifrons, and G. nana); it is supported by two synapomorphies and is relatively well resolved. Guttigadus nana is the most atypical member and appears to be paedomorphic with neotenic characteristics. Laemonema remains undefined by synapomorphies.

Key to adult Laemonema and Guttigadus (n = number of individuals).

1a.- Interorbital width 7.1-15 % SL 2

1b.- Interorbital width 3.0-7.0 % SL 6

2a.- Gill rakers on lower limb of first gill arch 22-30 (n=46) .... _G_. _globiceps_

(Chile, Argentina, South Africa, Australia, New Zealand)

2b.- Gill rakers on lower limb of first gill arch less than 22 3

3a.- Gill rakers on upper limb of first gill arch 3-5 (n=5) .... _G_. _nudicephalum_

(eastern South Africa)

3b.- More than 5 upper gill rakers on first arch 4

4a.- Gill chamber, floor of mouth, and lips pale (n=50) .... _G_. _kongi_

(Chile, Argentina, Southern Ocean, Australia, New Zealand)

4b.- Gill chamber, floor of mouth, and lips dark 5

5a.- Lower jaw included in upper jaw; scales on a straight line 111-137; scales below lateral line 27; lower gill rakers 17-22 (n=10) .... _G_. _globosus_

(New Zealand, subtropical South Atlantic)

5b.- Lower jaw not included in upper jaws; scales on a straight line 145-150; scales below lateral line 38; lower gill rakers 14-17 (n=22) .... _G_. _latifrons_

(North-eastern Atlantic, South-western Indian Ocean)

6a.- Upper gill rakers 1-2; caudal vertebrae 27-30 (n=11) .... _G_. _nana_

(Japan)

6b.- Upper gill rakers more than 2; caudal vertebrae 29-43 7

7a.- P1 with 16-24 rays 8

7b.- P1 with 25-31 rays 15

8a.- Caudal vertebrae 29-31, D1 with 8-9 rays (n=3) .... L. verecundum

(central Pacific, off Mexico)

8b.- Caudal vertebrae 34-43, D1 with less than 8 rays 9

9a.- P1 16-18, barbel absent (n=12) .... L. longipes

(North western Pacific, off Japan, Bering Sea)

9b.- P1 more than 18, barbel present 10

10a.- Scales on a straight line 150-172 (n=5) .... L. gracillipes

(tropical eastern Pacific)

10b.- Scales on a straight line less than 150 11

11a.- Lower gill rakers 10-13 12

11b.- Lower gill rakers greater than 13 13

12a.- Lower procurrent caudal fin rays 14-20, second fin ray of D1 elongated and black in adults; scales on a straight line 128-140 (n=79) .... L. barbatulum

(tropical and subtropical western North Atlantic)

12b.- Lower procurrent caudal fin ray 11-13, second fin ray of D1 not elongated and brown in adults; scales on a straight line 105-130 (n=20) .... L. rhodochir

(Kyushu-Palau Ridge, Hawaii, Sala y Gomez Ridge)

13a.- Upper portion of D1 and D2 with a black stripe (n=17) .... L. yarrelli

(subtropical eastern North Atlantic)

13b.- Upper portion of the D1 and D2 without a black stripe 14

14a.- D2 rays 63-72 (mode= 66); A rays 60-69 (mode= 64); total vertebrae 53 -58 (mode= 55) (n=44) .... L. laureysi

(subtropical and tropical eastern Atlantic)

14b.- D2 rays 66-73 (mode= 70); A 65-71 rays (mode= 67); total vertebrae with 56-59 (mode= 57) (n=50) ... L. n. sp. g

(subtropical and tropical western Atlantic)

15a.- P1 rays 31, highly modified scales on lateral line (n=1) .... L. yuvto

(Sala y Gomez Ridge)

15b.- P1 rays less than 31, no highly modified scales on lateral line 16

16a.- P2 rays more than 49 % SL, (n=3) .... L. n. sp. i

(western Indian Ocean)

16b.- P2 rays less than 49 % SL 17

17a.- D1 rays with 7; a triangular black spot on posterior tips of D2, A, a vertical black band on caudal fin (n=18) .... L. melanurum

(North western Atlantic)

17b.- D1 rays less than 7 rays; no triangular black spot on posterior tips of D2, A, a vertical black band on the caudal fin .... L. robustum

(tropical eastern Atlantic North Pacific and South western Pacific).

Taxonomic accounts

Laemonema Günther in Johnson, 1862

Laemonema Günther in Johnson, 1862:171 (type species Laemonema robustum Johnson, 1862 by monotypy).

Svetovidovia Cohen, 1973 in Hureau and Monod:326 (type species Gargilius lucullus Jensen, 1953).

Svetovidovia: Cohen, 1986:723. Fahay and Markle, 1984:265-272, Markle, 1989:83. Paulin, 1989:248.

Gargilius Jensen in Koefed, 1953:11 (type species Gargilius lucullus Jensen, 1953).

Lepidion (not of Swainson): Haedrich, 1964: 15 (juvenile reference for L. barbatulum).

Diagnosis: A morid fish with interorbital width equal to or shorter than orbit diameter; six to nine rays in first dorsal fin, with first dorsal ray almost always beneath skin; second dorsal fin with 40-73 rays; anal fin with 41-71 rays; teeth on vomer; caudal peduncle small and thin; chin barbel usually present; adults with two well-developed pelvic rays and two to nine small inner rays under the skin; photophores absent.

Comments: Günther in Nov 8, 1862, erected Laemonema for Phycis yarrelli Lowe. For many years it was believed that L. yarrelli was the type species of Laemonema. But on June 10, 1862, Johnson published a paper which described the genus Laemonema Günther MS and described a new species L. robustum (D. M. Cohen personal communication, 1989). According to the rules of Zoological Nomenclature, the genus was described by

Günther (in Johnson 1862) and the type species should be Laemonema robustum, a conclusion also reached by Eschmeyer (1990).

Three groups of Laemonema can be distinguished based on a principal components analysis of selected meristics: D2, A, PCV, P1, LGR and UGR (Fig. 21). One group contains L. barbatulum, L. n.sp. i, L. melanurum, L. robustum, L. rhodochir, and L. yuvto, characterized by a comparatively higher number of rays in P1, lower number of rays in D2 and A, and a lower number of UGR and LGR. A second group contains L. gracillipes, L. longipes, L. n.sp. g, L. laureysi, and L. yarrelli, characterized by a comparatively higher number of rays in D2, A, lower number of rays in P1, higher number of vertebrae in PCV, and higher number of rakers in UGR and LGR. The last group is monotypic containing only L. verecundum, which is characterized by the lower values for D2, A, and PCV.

Laemonema barbatulum Goode and Bean, 1883

(Fig. 22)

Laemonema barbatulum Goode and Bean, 1883:204-206.

Laemonema barbatula: Goode and Bean, 1896:362-363. Garman, 1899:188. Parin, 1984:57.

Gargilius vitellius Koefed, 1953:11.

Lotella maxillaris Bean, 1884: 241.

Diagnosis: Body low and slender, covered by small deciduous scales. Gill rakers 3-6 + 10-13, total= 14-18. Caudal fin

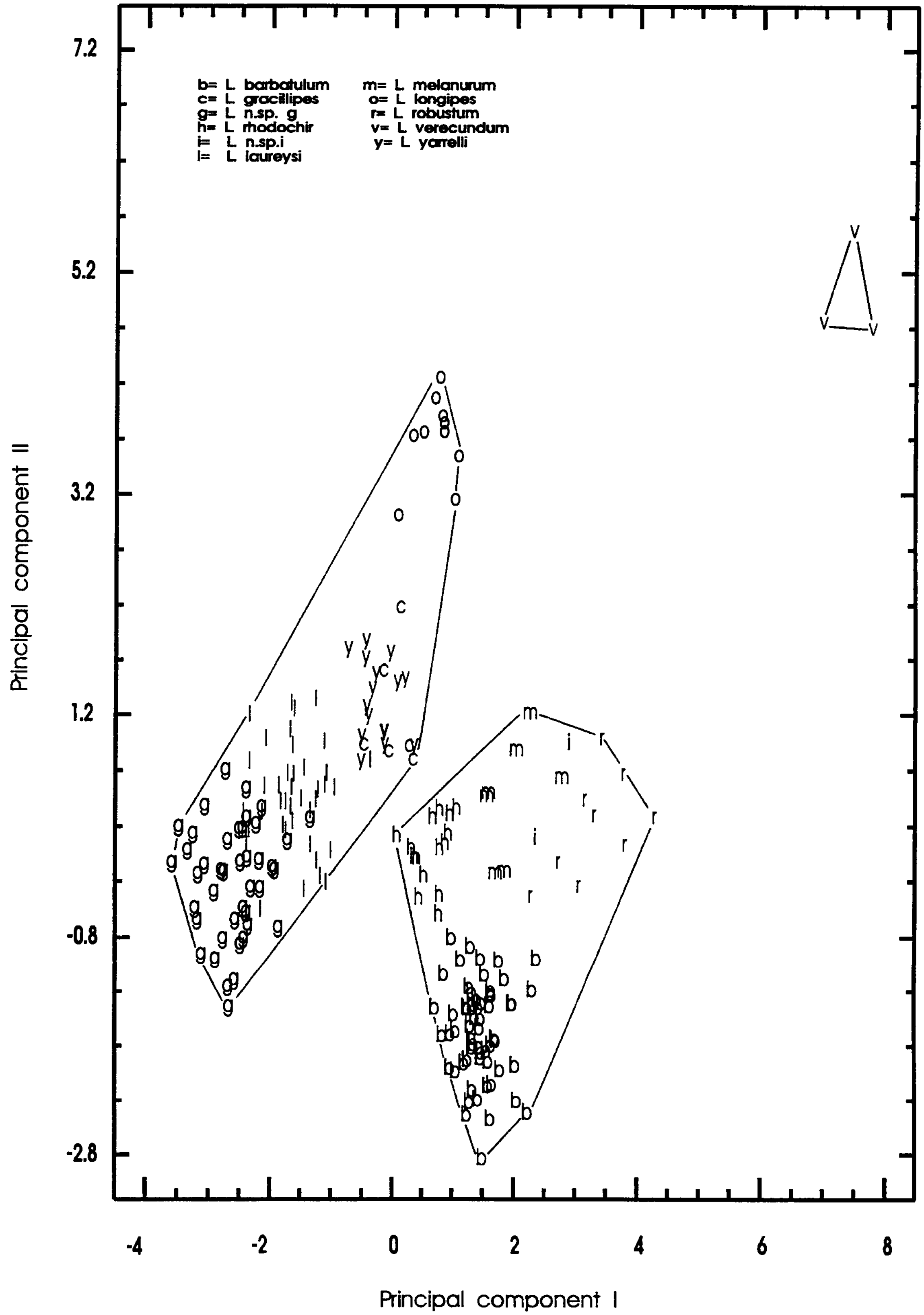


Fig. 21. Principal component analysis for meristic data (D2, A, PCV and CV) for Laemonema species.

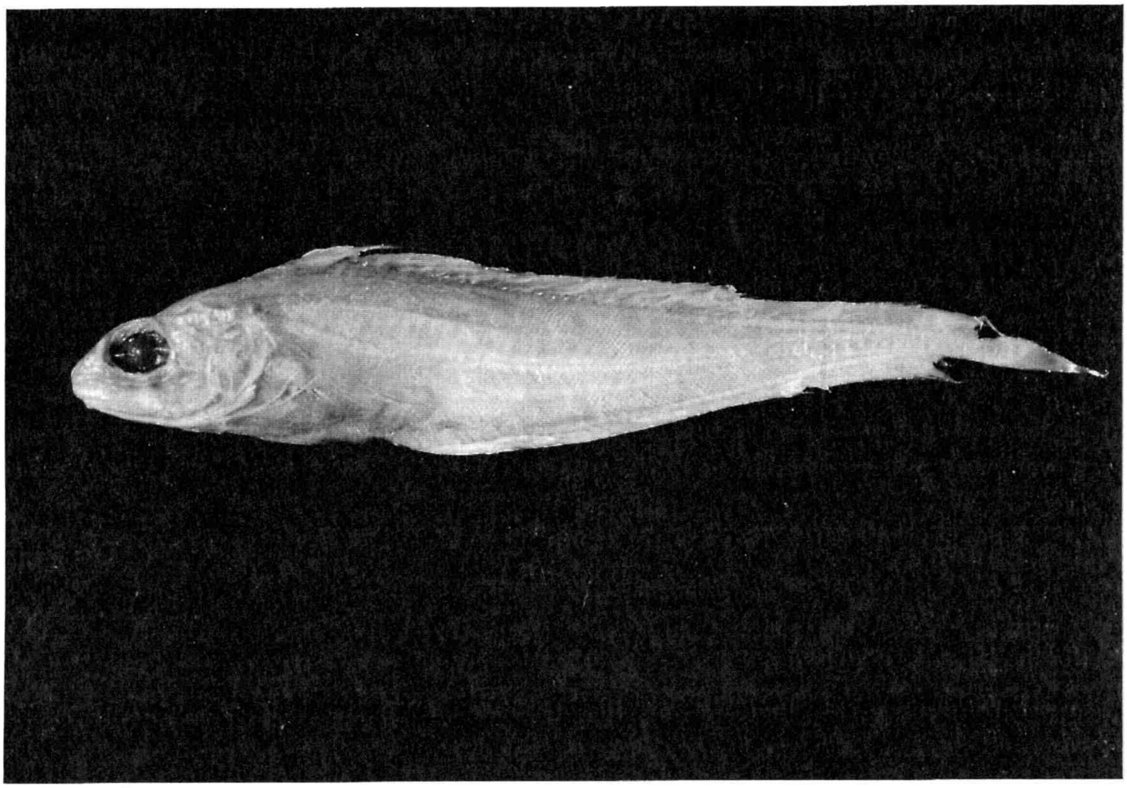


Fig. 22. Laemonema barbatulum Goode and Bean, 1883.
UF 13120 (125 mm SL)

with 7-9 + 6 + 14-20 rays. Black stripe on tips of dorsals and anal fin.

Description: Head 18.8-26.7 % SL, mouth subterminal. Snout short, 4.5-8.2 % SL. Maxillary with an external row of conspicuous canine-like teeth and two or three rows of small villiform teeth. Dentary with two rows of canine-like teeth, external teeth larger than internal teeth. Teeth on vomer canine-like, in a rounded patch. Chin barbel 1.3-5.0 % SL., smaller than orbit diameter. Orbit diameter 5.2-8.9 % SL, at least three times in head length. Interorbital narrow 3.9-6.1 % SL, almost four times in head length and almost twice in orbit diameter. Maxillary 7.7-12.7 % SL., ending about same level as the posterior end of pupil. Opercle bone ending in a flat spine in its upper portion. Postorbital length 8.2-11.1 % SL.

Greatest depth of body around area of anus, 13.8-38.1 % SL. Depth at first anal ray 13.2-28.4 % SL. Anus and anal fin separated by a short distance, smaller than height of caudal peduncle. Preanus length 32.7-57.0 % SL. Preanal fin length 35.0-56.5 % SL. Predorsal length 22.1-28.9 % SL. Depth at anus 11.1-25.4 % SL. Caudal peduncle depth 1.7-3.6 % SL.

First dorsal fin rays 6, except one individual with 7; base short 3.6-5.6 % SL. First ray beneath skin; second dorsal ray largest, 4.6-31.9 % SL, longer than head length in well-preserved specimens, remaining rays gradually decrease in length. Second dorsal fin rays 57-63 (X= 60.4, mode= 61, cv= 2.2), with large base 56.6-70.8 % SL., ray lengths gradually decrease from origin to insertion. Anal fin rays 54-63 (X= 58.1, mode= 58, cv= 2.9), shorter than second dorsal fin 43.5-61.9 % SL. Pectoral fin rays 19-23 (X= 21.0, mode= 21, cv= 3.8), prepectoral length 21.3-31.4 % SL, its base 2.9-5.6 % SL. In adults pelvic fin with two elongated rays; its length 6.9-37.0 % SL, not reaching vent; 2-3 small pelvic rays (X= 2.6, mode= 3, cv= 21.6) below the skin. Caudal fin asymmetrical, lower procurrent caudal fin rays 14-20 (X= 16.4, mode= 16, cv= 5.6), upper procurrent rays 7-9 (X= 8.0, mode= 8, cv= 6.3), principal rays 6 (X= 6.0, mode= 6). Total vertebrae 50-56 (X= 54.2, mode= 54, cv= 1.8), precaudal 13-15 (X= 14.9, mode= 14, cv= 3.2), caudal 37-42 (X= 40.0, mode= 40, cv= 2.2). Gill rakers 3-6 + 10-13, total = 14-18. Lateral line not well defined, on a straight line about 128-140 scales. Scales above lateral line 12-15 (X= 13.9, mode= 15, cv= 8.0), scales below lateral line 21-30 (X= 25.1, mode= 25, cv= 7.6).

Color in alcohol: This species has a yellowish to light brown body, dorsal and anal fins have a narrow black line along contours; second ray of first dorsal fin black.

Distribution: <u>Laemonema</u> <u>barbatulum</u> is distributed in the temperate western North Atlantic and tropical western Atlantic, from 40°17′ N, 50°39′ W to 02° 37′S, 41°03′W, over a depth of 50-1620 m (Fig. 23).

Comments: Koefoed (1953) described a new species <u>Gargilius</u> <u>vitellius</u> with the following meristic data: D1 5, D2 63, A

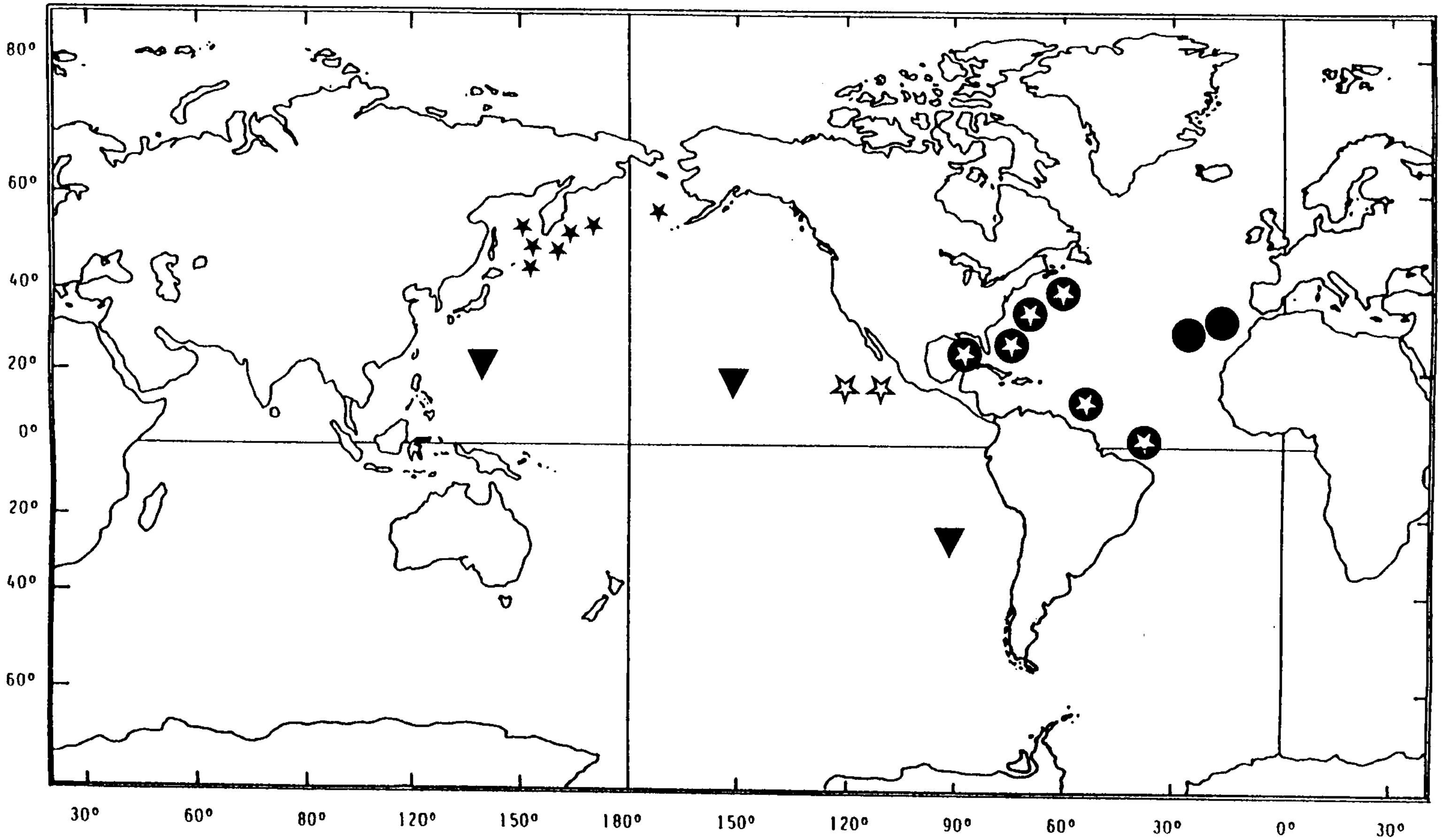


Fig. 23. Distribution map of Laemonema barbatulum (✪), Laemonema longipes (★), Laemonema rhodochir (▼), Laemonema verecundum (☆), and Laemonema yarrelli (●).

62, P1 17(r), 18(l), P2 10, and caudal rays 28 (7+9+12). Our counts from a radiograph of the holotype (Bergen Museum 4471, 47.9 mm SL) of G. vitellius showed the following: D1 6, D2 61, A 58, PCV 14, CV 40, TV 54, caudal rays 7+6+16. The following counts were taken directly from the specimen: P1 21, P2 11, GR 12+5. These data are similar to the meristic counts of juvenile specimens of L. barbatulum suggesting that Koefoed's specimen is a juvenile of L. barbatulum, based mainly on the disposition of caudal fin rays and color pattern, which had became lighter in alcohol.

Cohen (1986) described Svetovidovia because Gargilius Jensen was preoccupied; he indicated that the type species is G. lucullus. Svetovidovia vitellius (Koefoed, 1953) was tentatively referred to the juvenile stage of Laemonema by Fahay and Markle (1984), based on a transitional specimen showing ontogenetic loss of pelvic fin rays, but they did not assign S. vitellius to any known species of Laemonema. Svetovidovia Cohen is characterized by the presence of seven or more pelvic fin rays, a feature that apparently lead Haedrich (1964) to consider Svetovidovia to be juveniles of Lepidion.

Cohen (1979, and personal communication, 1989) examined Lotella and Physiculus from Japan and stated that Lotella maxillaris Bean was probably a juvenile Laemonema. Bean (1884) described Lotella maxillaris from the western North Atlantic. We examined the holotype of Lotella maxillaris (USNM 29832, 58.0 mm SL, head damaged) and obtained the following from an x-ray plate: D1 6, D2 61, A 58, PCV 14, CV 40, TV 54; and from direct examination: P1 22, P2 10, CR 8+6+16. The meristic data are within the range of juvenile specimens of L. barbatulum, suggesting that Lotella maxillaris is a juvenile of L. barbatulum.

Laemonema barbatulum is very similar to L. yarrelli but has fewer lower gill rakers (10-13 vs. 14-18), more lower procurrent caudal rays (14-20 vs 11-12), and more scales on a straight line (128-140 vs 100-111). Laemonema barbatulum is also similar to L. rhodochir but has more lower procurrent caudal fin rays (14-20 vs 11-13), a black stripe on the vertical fins, and an interarcual ligament which is not found in L. rhodochir. Laemonema barbatulum differs from L. robustum in having fewer scales below lateral line (21-30 vs 39-47), fewer upper procurrent caudal fin rays (7-9 vs 10-12), a "neck" between the two chambers of the gas bladder (the "neck" is absent in L. robustum), and a black stripe on the verticals fin. Laemonema barbatulum differs from L. n.sp. i, mainly in having fewer pectoral fin rays (19-23 vs 27), smaller pelvic fin rays (6.9-37.0 % SL vs 49.0-65.0 %), and a "neck" between the two chambers of the gas bladder. Laemonema barbatulum differs from L. melanurum in having fewer pectoral fin rays (19-23 vs 25-27), fewer scales above lateral line (12-15 vs 18), and fewer scales below lateral line (21-30 vs 35-36). It also lacks the triangular black patches on the upper end of the dorsal and anal fins, and rectangular black patch on the caudal fin found in L.

melanurum. Laemonema barbatulum differs from L. yuvto in having fewer pectoral fin rays (19-23 vs 31), no modified scales on lateral line, and black stripes on the vertical fins.

Juvenile stages of Laemonema barbatulum: The following description is based on the best-preserved specimens of several lots coming from many institutions. The stages are intended to be representatives and do not represent real steps in nature.

An individual of 81.6 mm SL (ARCH 049) considered a late juvenile of L. barbatulum, is yellowish on most of the body, the visceral region is dark blue, the edges of the first and mainly the second dorsal and anal fin are black, and has only two large visible pelvic fin rays.

A specimen of 64.8 mm SL (MCZ 59773) has only two large and strong pelvic rays. At 58 mm SL (MCZ 86752), it is possible to observe two long, plus four smaller, pelvic fin rays. A specimen 66 mm SL (MCZ 86752) has five larger and five smaller pelvic fin rays. At 60 mm SL (MCZ 85891) and less, individuals have normally 10 pelvic fin rays, all of them the same length.

The color of the body gradually varies from light yellow in specimens of 64 mm SL to dark brown in specimens of 60 to 12 mm SL. Individuals below 12 mm SL had a light brown body, with less amounts of pigmentation, more defined melanophores on the body, and the area of the head is less pigmented. Two pigmented lines, following the dorsal and ventral contours of the body, are evident in individuals of approximately 60 mm SL; one medial line becomes evident in individuals of 45 mm SL and smaller. The caudal peduncle and the caudal fin are without pigmentation in individuals of 75 mm SL to smaller ones. The pigmentation pattern on the fins changes from individuals of 60 mm SL, which presented the second dorsal and anal fins highly pigmented to less pigmented in individuals of 37 mm SL. A less pigmented state to an absence of pigments in the second dorsal and anal fin are found in individuals below 25 mm SL. In individuals about 40-50 mm SL the pelvic fin rays had melanophores. All fins are formed in individuals larger than 25 mm SL. In individuals of 38 mm SL, the second ray of the first dorsal fin starts to enlarge. Gill rakers are completely developed in specimens above 11 mm SL.

The smallest individual of L. barbatulum examined was 7.45 mm NL (A16 85-02 st 26 6B5). This prejuvenile has a large head (33.0 % NL) with big eyes (9.66 % NL), and the caudal skeleton is not yet formed. The deepest height of the body lies near the insertion of the pelvic fins. Dorsal and anal fins already have their normal number of rays. The pectoral fins have developed their normal number of rays (19-23). Ten pelvic fin rays are fully developed and normally found in this and other specimens at these smaller sizes. Gill arches are formed, but not gill rakers. Coloration of the body is as follows: the end of the tail has no melanophores, pigmentation increases towards the head; it is possible to observe three straight, dark-brown horizontal lines on the dorsal, lateral, and ventral surfaces of the posterior 1/3 of the body; the ventral line is largest. Pigmentation covers the area between these pigmented horizontal lines. On the anterior part of the body, there is a whitish vertical area with less pigmentation than posteriorly. In the area above and on the viscera, there is an area more pigmented than in posterior areas. The head has very little pigmentation.

Comments: The juveniles stages of L. barbatulum were identified based primarily on meristic characters (Table 5), supported by pigmentation pattern and the continuous decrease in size and number of inner pelvic fin rays, when fully developed the pelvic fins have only two rays (Fig. 24).

Material examined: ARC 8602169 (1, 43.7 mm SL), 38° 50'N, 54° 18'W, 50 m, 7 IV 1979. ARC 8707094 (1, 47.4 mm SL), 39° 58'N, 50° 32'W, 100 m, 26 IV 1979. ARC 8707128 (1, 59.4 mm SL), 42° 27'N, 62° 27'W, 100 m, 15 V 1979. ARC 8706054 (1, 70 mm SL), 42°16'N, 59°20'W, 30 VIII 1986. CAS 66824 (1, 59.5 mm SL), 32° 12'N, 64° 36'W, 900 fm. 15 VII 1930. MCZ 85890 (2, 38 mm SL), 39° 24'N, 69° 31'W, 0-780 m, 29 IV 1977. MCZ 85891 (1, 61.7 mm SL), 38° 29'N, 69° 05'W, 950 m, 16 VIII 1977. MCZ 85905 (3, 28-42.5 mm SL), 38° 31'N, 72°23', 0-250 m. 26 IV 1982. MCZ 38310 (1, 72.8 mm SL), 40° 43'N, 66° 39'W, 600-650 fms, 25 VII 1953. UF 12934 (2, 60-120 mm SL), 28° 58'N, 79° 57'W, 225 fm, 18 II 1965. UF 13120 (24, 90-130 mm SL) (one specimen cleared and stained), 28° 50'N, 79° 54'W, 204-216 fm, 21 II 1965. UF 37729 (1, 145 mm SL), 24° 21'N, 81° 48'W, 236 m, 21 IV 1980. UF 41031 (11, 90-175 mm SL), 30° 10'N, 80° 08'W, 150 fm, 25 V 1984. USNM 155735 (3, 75-155 mm SL), 28° 08'N, 79° 54'W, 30 III 1940. USNM 29045 (1), X-ray plate. VIMS 6293 (8, 60-105 mm SL). ZMB 4471 (1, 57 mm SL), 40° 17'N, 50° 39'W, 2200 mwo, 27 VI 1910 (holotype of Gargilius vitellius).

Table 5.- Comparison between selected meristic characters of adults and juveniles of <u>Laemonema barbatulum</u>

	range size (mm)	D2							A									
		57	58	59	60	61	62	63	54	55	56	57	58	59	60	61	62	63
<u>L</u>. <u>barbatulum</u>	>75	1	1	4	12	10	6	1		1	1	6	12	10	2	2		
<u>L</u>. <u>barbatulum</u>	<75	1	3	2	7	11	6	2	1	3	1	7	10	4	2	2		1

		P1					P2							PCV				
		19	20	21	22	23	2	*	7	8	9	10	11	13	14	15	16	17
<u>L</u>. <u>barbatulum</u>	>75		5	20	10	1	36								28	6		
<u>L</u>. <u>barbatulum</u>	<75	2	11	19	6	1	2		1	1	3	19	12	2	22	8		1

		CV						TV							LGR				
		37	38	39	40	41	42	50	51	52	53	54	55	56	10	11	12	13	14
<u>L</u>. <u>barbatulum</u>	>75			2	23	8	1				2	18	13	2	1	14	22		
<u>L</u>. <u>barbatulum</u>	<75	1	3	7	11	6	1	1		2	4	13	8	2	1	14	19	1	1

		UGR				UPPCR			LPCR						
		3	4	5	6	7	8	9	14	15	16	17	18	19	20
<u>L</u>. <u>barbatulum</u>	>75	1	21	14		4	24	4	1	14	13	2		1	
<u>L</u>. <u>barbatulum</u>	<75	13	21	2	1	7	19	5	1	4	19	3	4		1

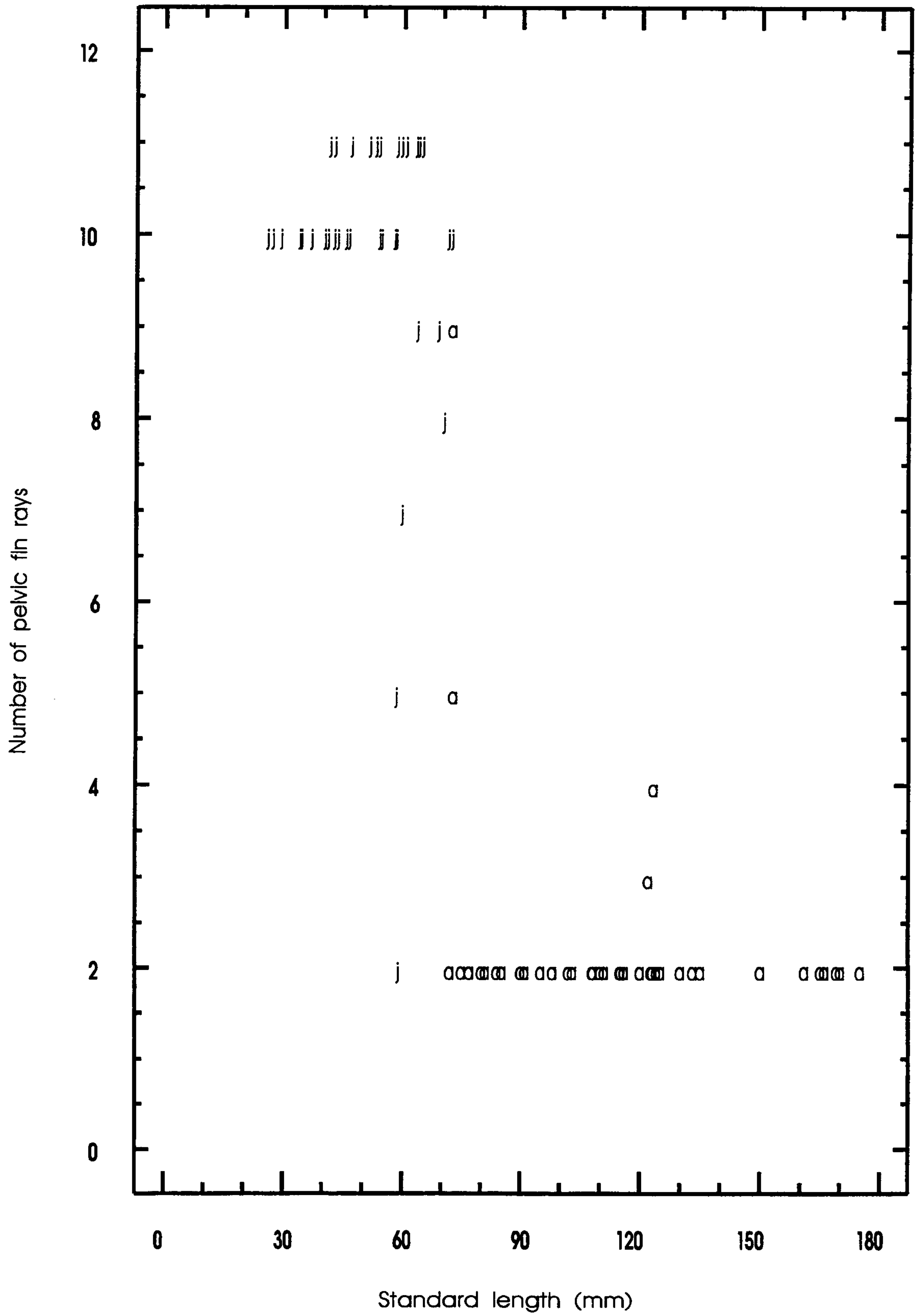


Fig. 24. Number of pelvic fin rays vs Standard length in L. barbatulum (a=adults, j= juveniles).

Other material of L. barbatulum examined but not included in analysis: MCZ 86752 (1, 64.3 mm SL), 41° 53'N, 64° 23'W, 4000 mwo, 28 VII 1953. MCZ 86753 (1, 72.5 mm SL), 38° 39'N, 71° 54'W, 750-1000 m, 24 X 1977. MCZ 86754 (2, 59-59.2 mm SL), ca. 39°N, 70°W, V 1976. MCZ 86755 (1, 64.9 mm SL), 39° 00'N, 70° 00'W, 3 X 1936. MCZ 85773 (1, 60.9 mm SL), 37° 12'N, 74° 18'W, 751-1000 m, 17 VIII 1982. MCZ 85813 (1, 64.3 mm SL), 37° 06'N, 73° 45'W, 755-1000 m, 26 VI 1982. MCZ 85814 (1, 61.3 mm SL), 36° 37'N, 73° 44'W, 0-1082 m, 10 VIII 1982. MCZ 85815 (1, 60.5 mm SL), 37° 07'N, 73° 39'W, 797-994 m, 14 VIII 1982. MCZ 85888 (1, juvenile), 36° 30'N, 67° 57'W, 750 -1000 m, 23 IV 1977. MCZ 85889 (1, juvenile), 38° 21'N, 67° 37'W, 0-1020 m, 28 IV 1977. MCZ 85895 (1, juvenile), 34° 24'N, 75° 50'W, 190-2690 m, 23 IV 1970. MCZ 85896 (1, juvenile), no data available. MCZ 85901 (1, juvenile), 39° 13'N, 69° 35'W, 0-1022 m, 19 IV 1982. MCZ 85902 (1, juvenile), 39° 17'N, 69° 32'W, 0-1026 m, 20 IV 1982. MCZ 85903 (1, 31.5 mm SL), 38° 39'N, 72° 23'W, 0-1029 m, 24 IV 1982. MCZ 85904 (6, 15.6-39.3 mm SL), 38° 31'N, 72° 23'W, 0-1032 m, 24 IV 1982. MCZ 85096 (1, tail broken), 38° 34'N, 72° 31'W, 0-1006 m. 26 IV 1982. MCZ 85097 (1, 42 mm SL), 39° 13'N, 71° 17'W, 153-503 m, 16 VI 1982. MCZ 38088 (1, juvenile), 39° 59'N, 70° 38'W, 180-220 fms, 16 X 1948. MCZ 40930 (2, juvenile), 27° 14'N), 79° 50'W, 210 fms, 29 VII 1957. MCZ 65166 (1, 182 mm Sl), 34° 46'N, 75° 27'W, 306-305 m, 4 III 1984. MCZ 25840 (1, juvenile), 32° 43'N, 77° 20'W, 233 fms, 16 VII 1880. MCZ 25842 (3, juvenile), 32° 07'N, 78° 37'W, 229 fms, 17 II 1880. MCZ 38303 (1, 100 mm SL), 38° 08'N, 73° 45'W, 200-275 fms, 28 VI 1953. MCZ 45370 (2, juvenile), 25° 15'N, 80° 01'W, 160 fms, 22 VII 1957. MCZ 45377 (1, juvenile), 29° 43'N, 80° 09'W, 200 fms, 20 XI 1957. CAS-SU 44952 (1, 70 mm SL), (same CAS 66824). CAS-SU 63261 (1, 246 mm SL), 29° 43'N, 80° 09'W, off Florida, 21 XI 1957. UF 12899 (6), 29° 04'N, 80° 00'W, 220 fm, 15 II 1965. UF 12944 (1), 28° 39'N, 79° 55'W, 200-205 fm 22 II 1965. UF 13024 (7, 106-132 mm Sl), 29° 13'N, 79° 56'W, 300 fm, 19 II 1965. UF 13030 (5, 110-127 mm SL), (same as UF 12899). UF 27461 (2, 160 mm Sl plus broken tail), 32° 31'N, 78° 30'W, 135 fm, 26 IX 1979. UF 39844 (2, 60 -67 mm SL), 34° 18'W, 75° 50'W, 207-220 fm, 15 V 1983. UF 39937 (3, 90-104 mm SL), 24° 48'N, 80° 12'W, 200 fm, 9 XI 1961. UF 39941 (2, 70-90 mm SL), 29° 52'N, 80° 08'W, 200 fm, 27 IV 1957. UF 41125 (10, 80-140 mm SL), 29° 39'N, 80° 05'W, 225 fm, 29 V 1984. UF 45179 (1, 160 mm SL), 30° 20'N, 80° 03'W, 190-191 fm, 21 I 1986. UF 45374 (1, 67 mm SL), 29° 53'N, 80° 11'W, 170-180 fm, 17 I 1962. UF 45375 (1, 55 mm SL), 29° 22'N, 80° 05'W, 200 fm, 24 XI 1957. UF 45377 (1, 75 mm SL), 32° 51'N, 77° 31'W, 170 fm, 19 IV 1957. UF 45380 (1, 64 mm SL), 29° 48'N, 80° 12'W, 210 fm, 14 VIII 1957. UF 45452 (1, 72 mm SL), 29° 30'N, 80° 10'W, 160 fm, 14 VIII 1957. UF 45454 (1, 68-85 mm SL), 32° 40'N, 77° 40'W, 21 IV 1957. UF 39864 (1, 63 mm SL), 34° 19'N, 75° 49'W, 201-221 fm, 15 V 1983. UF 39938 (2, 100-120 mm SL), 30° 03'N, 80° 09'W, 180 fm, 22 VIII 1962. UF 41022 (1, 75 mm SL), 28° 30'N, 79° 55'W, 125 fm, 23 V 1984. UF 41138 (1, 85-109 mm SL), 29° 30'N, 80° 09'W, 175 fm, 29 V 1984. UF 41200 (5, 90-140 mm SL), 28° 00'N, 79° 56'W, 200 fm, 30 V 1984. UF 45372 (1, 80 mm SL), 31° 31'N, 79° 27'W, 220 fm, 23 IV 1957. UF 45376 (1, 65 mm SL), 29° 27'N, 80° 07'W, 190-192 fm, 28 IV 1961. UF 45378 (2, 66-72 mm SL), 28° 50'N, 80° 00'W, 100 fm, 2 II 1961. UF 45379 (2, 62-70 mm SL), 32° 50'N, 77° 27'W, 200 fm, 21 IV 1957. UF 45453 (1, 74 mm SL), 29° 15'N, 80° 05' W, 210 fm, 31 V 1957. UF 45455 (1, 71 mm SL), 33° 23'N, 76° 43'W, 210 fm, 20 IV 1957. UF 45456 (1, 72 mm SL), 32° 50'N, 77° 27'W, 200 fm, 21 IV 1957. UF 45457 (16, 72-137 mm SL), 30° 13'W, 80° 05'W, 220 fm, 26 IV 1957. UF 63666 (5, 77-136 mm SL), 24° 13'N, 81° 42'W, 300 fm, 21 VII 1957. USNM 304670 (1, 115 mm SL), 24° 29'N, 83° 33'W, 200 fm, 22 XI 1963. USNM 304669 (1, 149 mm SL), 24° 28'N, 83° 29'W, 210 fm, 22 XI 1963. USNM 304667 (1, 150 mm SL), 29° 54'N, 80° 10'W, 190 fm, 9 II 1965. USNM 304666 (1, 130 mm SL), 29° 29'N, 80° 08'W, 210 fm, 18 VIII 1957. USNM 304665 (5, 67-145 mm SL), 29° 50'N, 80° 10'W, 155 fm, 25 I 1960. USNM 304664 (3, 125-154 mm SL), 24° 30'N, 83° 34'W. 27 11 1963. USNM 304663 (1, 81 mm SL), 29° 47'N, 80° 12'W, 153 fm, 10 VI 1956. USNM 304662 (9, 104-165 mm SL), 24° 28'N, 83° 33'W, 210 fm 22 XI 1963. USNM 158752 (1, 154 mm SL), 28° 22'N, 79° 53'W, 11 III 1956. USNM 158112 (1, 156 mm SL), (same USNM 158752). USNM 158108 (3, 73-102 mm SL), 26° 18'N, 79° 51'W, 200 fm, 29 III 1956. USNM 158106 (1, 73 mm SL), 29° 36'N, 80° 06'W, 180 fm, 10 IV 1956. USNM 148362 (1, 64 mm SL), 38° 29'N, 70° 54'W, 18 IX 1886. USNM 304651 (34, 75-82 mm SL), 26° 39'N, 79° 30'W, 10 XI 1960. USNM 304644 (1, 149 mm SL), 29° 13'N, 79° 59'W, 205 fm, 2 V 1960. USNM 304645 (2, 70-82 mm SL), 24° 25'N, 83° 29'W, 14 XII 1962. USNM 304642 (3), 24° 27'N, 83° 24'W, 220 fm, 23 XI 1963. USNM 304637 (6), 36° 42'N, 74° 36'W, 605 m, 16 XI 1974. USNM 158232 (3, 138-172 mm SL), 22° 40'N, 86° 36'W, 206 fm, 19 VI 1952. USNM 158088 (1, 78 mm SL), 28° 03'N, 79° 52'W, 150 fm, 8 IV 1956. USNM 304621 (2, 164-122 mm SL), 24° 26'N, 83° 30'W, 260 fm, 26 XI 1965. USNM 304606 (4, 124-157 mm SL), 24° 26'N, 83° 23'W, 200 fm, 22 XI 1963. USNM 304605 (3, 70-72 mm SL), 24° 13'N, 81° 24'W, 28 X 1960. USNM 304604 (1, 84 mm SL), 29° 14'N, 80° 05'W, 205 fm, 15 XI 1964. USNM 304603 (6, 80-140 mm SL), 24° 24'N, 82° 28'W, 12 XII 1962. USNM 304602 (1, 92.0 mm SL), 24° 18'N, 81° 29'W, 28 X 1960. USNM 304601 (3, 111-118 mm SL), 24° 30'N, 83° 32'W, 190 fm, 26 XI 1963. USNM 304600 (1, 117 mm SL), 28° 50'N, 79° 54'W, 19 II 1965. USNM 304599 (1, 89.2 mm SL), 23° 56'N, 87° 32'W, 5 VI 1959. USNM 304598 (1, 113 mm SL), 28° 31'N, 79° 52'W, 180 fm, 28 IV 1957. USNM 304597 (1, 76.4 mm SL), 24° 14'N, 81° 24'W, 28 X 1960. USNM 304596 (5, 83-124 mm SL), 2° 37'S, 41° 03'W, 16 fm 12 III 1963. USNM 304595 (1, 128 mm SL), 24° 26'N, 83° 23'W, 190 fm, 26 VII 1963. USNM 304594 (3, 91-112 mm SL), 29° 40'N, 80° 12'W, 200 fm, 13 XI 1964. USNM 304593 (4, 80-97 mm SL), 29° 36'N, 80° 10'W, 190 fm, 17 VI 1958. USNM 304592 (1, 112 mm SL), 32° 15'N, 78° 51'W, 169 fm, 23 I 1972. USNM 304591 (1, 136 mm SL), 29° 58'N, 80° 08'W, 200 fm, 05 II 1964. USNM 304590 (1, 78 mm SL), 29° 57'N, 80° 07'W, 200 fm, 5 II 1964. USNM 304589 (3, 64-107 mm SL), 29° 03'N, 80° 00'W, 190 fm, 10 II 1965. USNM 304588 (7, 75-133 mm SL), 20° 48'N, 70° 46'W, 210 fm, 28 V 1965. USNM 304587 (10, 74-123 mm SL), 29° 13'N, 79° 56'W, 300 fm, 18 II 1965. USNM 304586 (3, 78-130 mm SL), 29° 39'N, 80° 11'W, 190 fm, 10 II 1965. USNM 304585 (11, 74-112 mm SL), 28° 41'N, 79° 52'W, 28 IV 1961. USNM 304584 (2), 24° 30'N, 83° 32'W, 190 fm, 26 XI 1963. USNM 304583 (3, 138-145 mm SL), 29° 59'N, 80° 08'W, 210 fm, 9 II 1965. USNM 185053 (1), 24° 20'N, 83° 20'W, 190 fm, 13 IV 1954. USNM 304574 (3, 72.6-81.3 mm SL), 24° 18'N, 83° 18'W, 100 fm, 2 XII 1963. USNM 304553 (1), 7° 38'N, 54° 43'W, 250 fm, 7 XI 1957. USNM 45968 (1), 29° 03'N, 88° 16'W, 11 II 1885. VIMS 3691 (2, 95-110 mm SL).

Laemonema n.sp. g

(Fig. 25)

Diagnosis: Second dorsal fin with 66-73 rays, modally 70; height of first dorsal fin 10.1-17.1 % SL, with an average of 13.8 % SL; narrow interorbital 3.4-4.7 % SL; orbit diameter 6.4-8.3 % SL.

Description: Body fusiform, covered with moderate-sized scales. Head short, 20.0-24.0 % SL; maxillary 9.2-11.7 % SL, almost reaching middle of pupil, with one outer row of strong caniniform teeth followed by five or six rows of small inner teeth. Vomer with a rounded patch of teeth. Dentary teeth pattern same as for maxillary, but with two or three rows of small inner teeth. Orbit diameter greater than the interorbital width, 3.4-4.7 % SL. Postorbital length 8.8-10.7 % SL, the opercle ending in a flat and wide spine.

Predorsal length 21.4-27.6 % SL, D1 inserted at about same height as pectoral fin. Prepectoral length 20.5-26.0 % SL. Preanal length 37.8-45.7 % SL, anus close to anal fin, preanus length 35.5-44.0 % SL. Maximum depth of body around

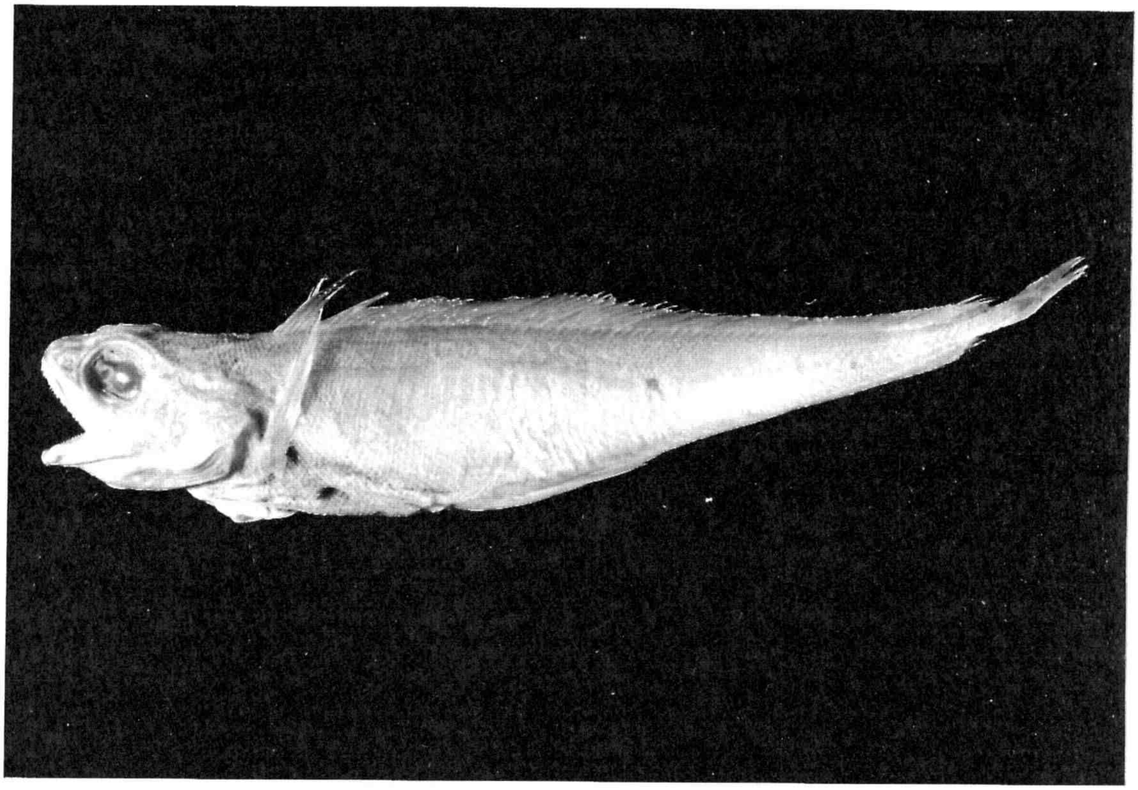


Fig. 25. Laemonema n.sp. g Paratype
UF 45373 (244 mm SL)

area of anus, 14.0-20.6 % SL. Body depth at first anal fin ray 12.2-19.3 % SL. Caudal peduncle depth 1.7 -2.5 % SL.

First dorsal fin with six rays (one specimen with five), the first ray beneath skin; second ray largest. Dorsal fin base 3.0-7.9 % SL. Second dorsal fin with 66-73 rays (X= 69.6, mode= 70, cv= 2.3), its base 63.4-71.0 % SL. Anal fin with 65-71 rays (X= 68, mode= 67, cv=2.5), its base 51.8-59.9 % SL. Pectoral fin with 19-22 rays (X= 20.3, mode= 20, cv= 3.5), its base 2.5-3.7 % SL, its length 12.0-17.3 % SL; inserted before insertion of first dorsal fin; prepectoral length 20.5-26.0 % SL. Pelvic fin with two rays, which reach fourth or fifth anal ray; fins inserted well before pectoral fin. Prepelvic length 14.7-24.7 % SL. Caudal fin asymmetrical, upper procurrent rays 8-11 (X= 8.6, mode= 9, cv= 7.9), six principal caudal rays, lower procurrent rays 12-16 (X= 14.0, mode= 14, cv= 6.9). Total vertebrae 56-59 (X= 57.6, mode= 57, cv= 1.5), precaudal vertebrae 15-17 (X= 16.2, mode= 16, cv= 2.9), caudal vertebrae 39-43 (x= 41.3, mode=41, cv= 2.2). Gill rakers 7-9 (X= 7.8, mode= 9, cv= 7.0) + 17-20 (X= 18.3, mode= 18, cv= 4.6), total= 24-29. Scales on a straight line 125-143; scales above lateral line 10-13 (X= 11.6, mode= 12, cv= 10.2).

Color in alcohol: This species has a light gray to withish body in older preserved specimens to a ligth pinkish body, in relatively new specimens. All fins are dusty brown to withish, with exception of first dorsal fin which have most of their rays tips black.

Distribution: Laemonema n.sp. g is widely distributed in the western Atlantic, from off Canada 42°38'N, 64°19'W to off southern Brazil, 25° 24'S, 44°54'W, including the Gulf of Mexico, off French Guiana, and off Suriname; depth range 180-792 m (Fig. 26).

Comments: This species is very similar to the allopatric L. laureysi Poll from the subtropical and tropical eastern Atlantic. Although there is overlap in most characters, they occupy different multivariate space based on both morphometric and meristic characters. Principal components analysis of HL, PDL, PAL, PANUS, UJL, SNT, ORB, INT, D2L, AL, and CAUDDEPTH separated the two groups, with few specimens of L. laureysi overlapping L. n.sp. g (Fig. 27). Discriminant analysis of these morphometric characters correctly distinguished all specimens. Principal component analysis of meristic characters D1, D2, A, P1, PCV, CV, UGR, LGR, UPPCR, and LPCR also separated the two species, but with more overlap (Fig. 28). Discriminant analysis using the meristic characters correctly distinguished 100 % of L. n.sp. g and 94.24 % of L. laureysi.

Description of a juvenile of Laemonema n.sp. g (MCZ 85898 44.2 mm SL): Body slender, head 24.0 % SL, orbit diameter 7.2 % SL, interorbital width 5.0 % SL. Predorsal length 27.6 % SL, prepelvic length 17.0 %, preanus length 39.1 % SL, preanal fin length 41.9 % SL, D2 length 64.5 %, A length 53.8 % SL, caudal peduncle depth 2.3 % SL.

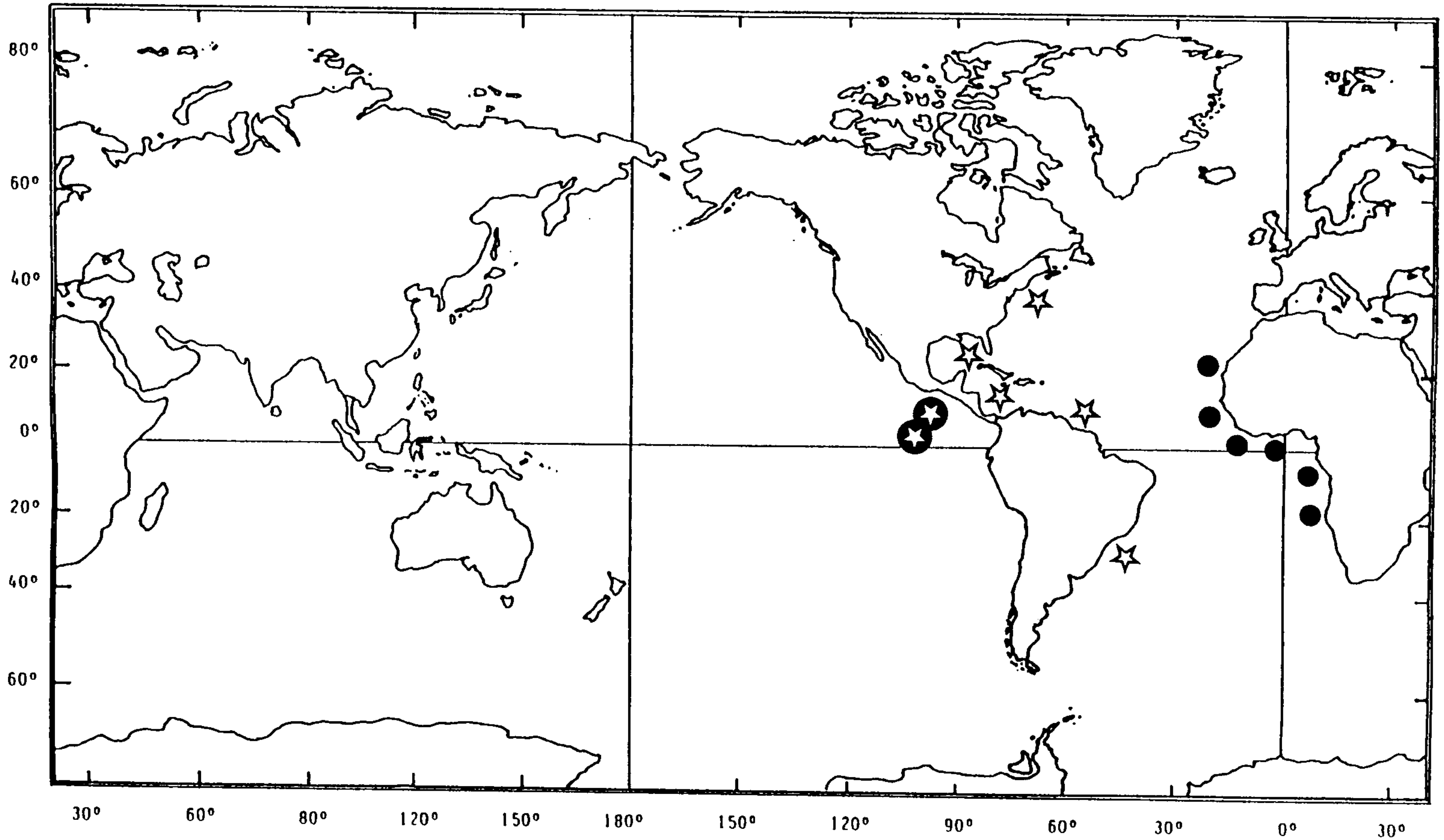


Fig. 26. Distribution map of Laemonema n.sp. g (☆), Laemonema gracillipes (✪), and Laemonema laureysi (●).

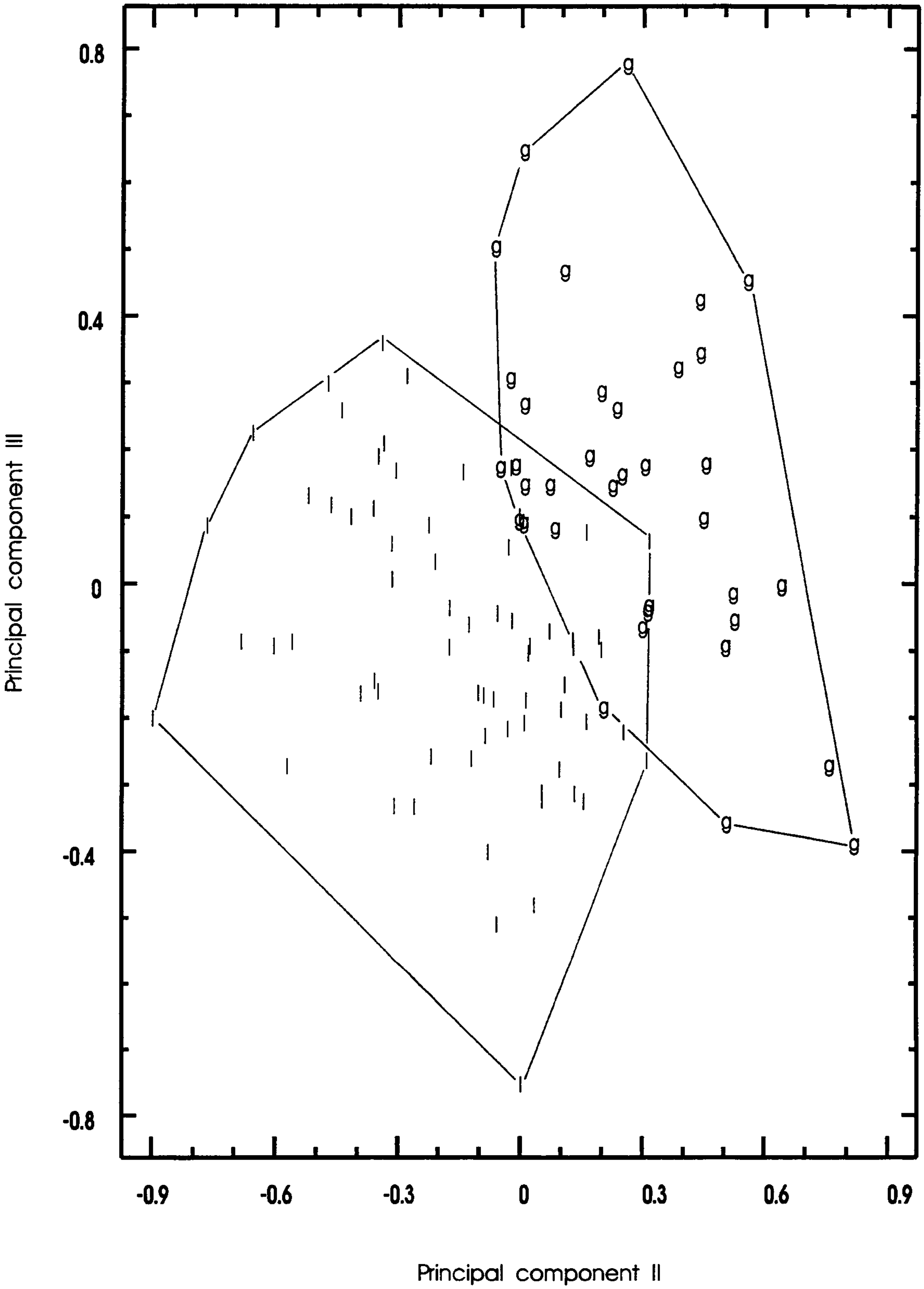


Fig. 27. Principal component analysis for morphometric characters for L. laureysi (l) and L. n.sp. g (g).

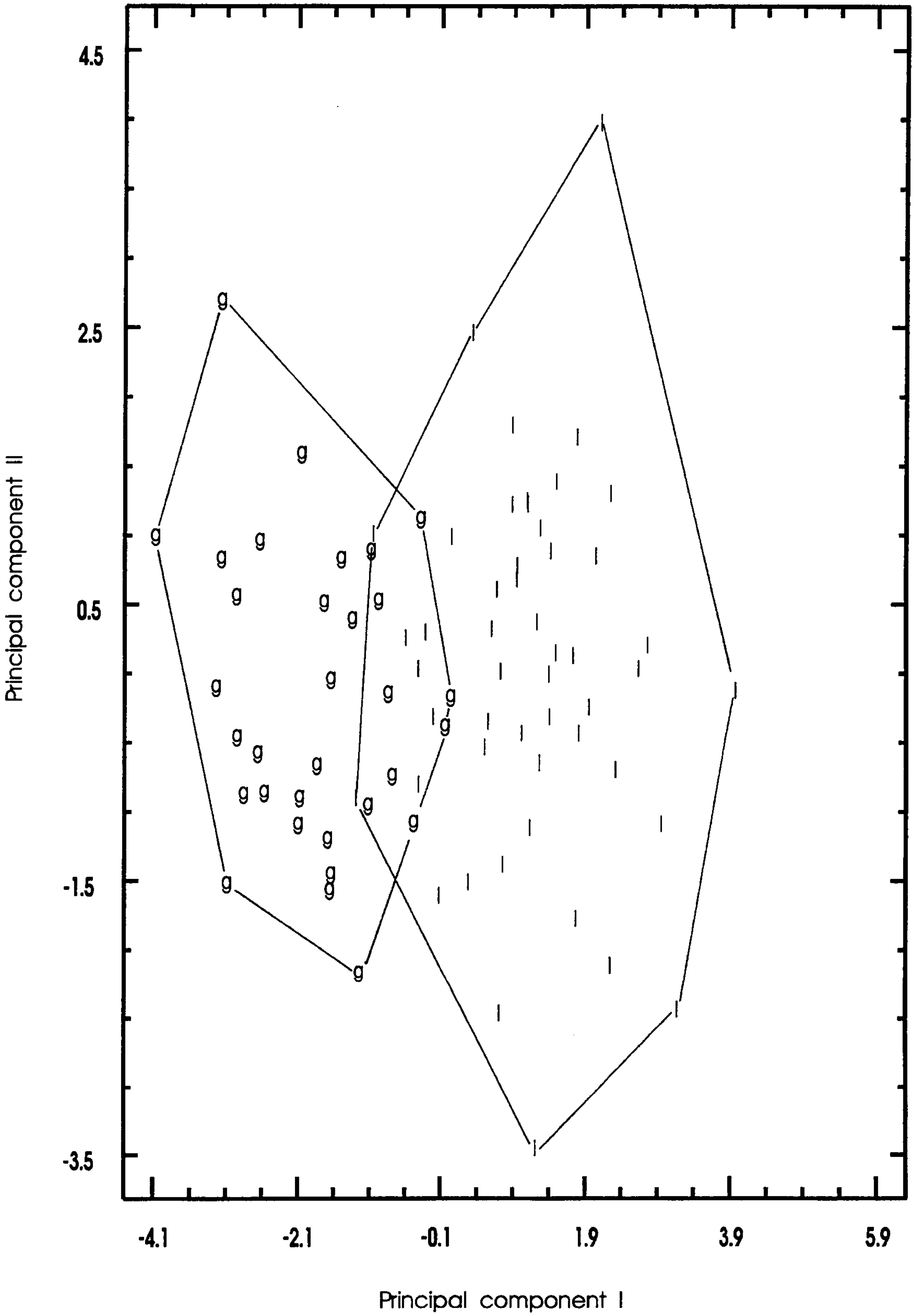


Fig. 28. Principal component analysis for meristic characters for L. laureysi (l) and L. n.sp. g (g).

First dorsal fin rays six, second dorsal fin with rays 71, anal fin rays 65, pectoral fin rays 21, pelvic fin rays seven. Caudal fin asymmetrical, upper procurrent caudal rays 9, principal caudal rays 6, lower procurrent caudal rays 14. Total vertebrae 57, precaudal vertebrae 16, caudal vertebrae 41. Gill rakers 8 + 17.

Color of body light brown; area of viscera brown; head paler than body, also on dentary and floor of mouth; highly pigmented area between insertion of pelvic fins. Pelvic fins have melanophores over entire length. Most conspicuous character is pattern of rectangular spots of brown pigment that contrast with white second dorsal and anal fins. Usually possible to count five spots on second dorsal and seven spots on anal fin. At this size, there is a small area the end of caudal skeleton without pigmentation.

Laemonema n. sp. g differs from other similar species in having more second dorsal fin rays (66-73) compared to *L. gracillipes* (56-63), *L. yarrelli* (58-62), and *L. longipes* (49-53); more anal fin rays (65-71) compared to *L. gracillipes* (55-61), *L. yarrelli* (57-62), and *L. longipes* (48-52); more total vertebrae (56-59) compared *L. yarrelli* (52-54); fewer lateral line scales (125-143) compared to *L. gracillipes* (155-172), *L. yarrelli* (100-111); and a rounded vomer compared to the v-shaped vomer of *L. longipes*. Proposed type material : Holotype: USNM 045967, female, (169 mm SL), 28° 34'N, 86° 48'W, 11 II 1885. Paratypes: USNM 158228 (1, 236 mm SL), 29° 11'N, 86° 52'W, 24 II 1951. USNM

213496 (1, 149 mm SL), 36° 58'N, 74° 38'W, 613 -710 m, 17 IV 1974. USNM 158090 (1, 104.7 mm SL), 29° 10'N, 88° 07'W, 24 VI 1956. USNM 304409 (1, 92.3 mm SL), 09° 47'N, 79° 25'W, 230 fm, 19 X 1965. UF 44376 (2, 137-221 mm SL), 29° 09'N, 88° 03'W, 190-191 fm, 21 I 1986. UF 45373 (1, 244 mm SL), 14° 10'N, 81° 50'W, 300-330 fm, 21 V 1962. MCZ 57923 (1, 186 mm SL), 11° 36'N, 62° 46'W, 290 fms, 19 IV 1960., MCZ 45983 (1, 198 mm SL), 11° 53'N, 69° 25'W, 350 fms, 3 X 1963., LACM 43471-1 (2, 139-140 mm SL), ARC 8600883 (3, 207-262-269 mm SL), 42° 38'N, 64° 19'W, 360 m, 30 VIII 1986.

Material examined: ARC 8600821 (1, 190 mm SL), 42° 55'N, 61° 43'W, 585 m, 4 XI 1984. ISH 1066/66 (2, 165-182 mm SL), 33°35'S, 51°22'W, 450 m, 11 VI 1966. ISH 1887/68 (2, 120-228 mm SL), 25° 24'S, 44° 54'W, 500 m, 1 III 1968. MCZ 85898 (1, 44.2 mm SL), 39° 04'N, 68° 00'W, 199-196 m, 15 X 1982. UF 39976 (2, 112-125 mm SL), 27° 34'N, 93° 06'W, 225 fm, 11 VIII 1983. UF 39993 (2, 158-202 mm SL), 27° 33'N, 93° 10'W, 237 fm, 11 VIII 1983. UF 40041 (2, 180-219 mm SL), 27° 32'N, 93° 27'W, 288 fm, 12 VIII 1983. UF 40126 (1, 203 mm SL), 27° 25'N, 95° 54'W, 205 fm, 19 VIII 1983. UF 40284 (2, 209-216 mm SL), 26° 13'N, 96° 13'W, 150 fm, 25 V 1984. UF 44376 (4, 87-246 mm SL), 29° 09'N, 88° 03'W, 190-191 fm, 21 I 1986, (one specimen cleared and stained). UF 45373 (2, 244-255 mm SL), 14° 10'N, 81° 50'W, 300-330 fm, 21 V 1962. UF 39956 (1, 217 mm SL), 27° 35'N, 93° 01'W, 187 fms, 10 VIII 1983. USNM 45965 (1, 225 mm SL), 11° 43'N, 69° 09'W, 18 II 1884. USNM 45968 (1, 91.7 mm SL), 29° 03'N, 88° 16W, 11 II 1885. USNM 44231 (2, 220-227 mm SL), 29° 03'N, 88° 16'W. 11 II 1985. USNM 304410 (1, 77.2 mm SL), 24° 25'N, 87° 38'W, 406 fm, 9 VII 1970.

Other material of <u>Laemonema</u> n.sp. g examined but not included in the analysis: MCZ 53989 (2), 39° 28'N, 72° 18'N, 260-342 m, 28 II 1973. USNM 304706 (1, 150 mm SL), 13° 07'N, 82° 08'W, 300 fm, 13 IX 1957. USNM 304682 (5, 111-190 mm SL), 29° 08'N, 88° 13'W, 250 fm, 23 X 1962. USNM 304733 (1), 09° 15'N, 81° 32'W, 25 V 1962. USNM 304732 (1, 110 mm SL), 29° 08'N, 88° 13'W, 25 II 1969. USNM 304731 (1, 118 mm SL), 23° 28'N, 97° 13'W, 10 IV 1964. USNM 304730 (1, 141 mm SL), 29° 04'N, 88° 26'W, 200 fm, 27 X 1962. USNM 304729 (1, 97 mm SL), 12° 01'N, 61° 53'W, 210 fm, 26 IX 1964. USNM 304728 (1, 179 mm SL), 24° 17'N, 87° 35'W, 300 fm, 10 VIII 1970. USNM 304727 (1, 111 mm SL), 11° 54'N, 69° 23'W, 3 X 1963. USNM

304726 (1, 185 mm SL), 12° 19'N, 72° 34'W, 195 fm, 20 XI 1970. USNM 304724 (1), 16° 51'N, 82° 14'W, 320 fm, 15 XI 1968. USNM 304723 (3, 193-168 mm SL), 16° 57'N, 81° 19'W, 7 VI 1962. USNM 304722 (1, 217 mm SL), 09° 13'N, 81° 30'W, 200 fm, 25 V 1962. USNM 304721 (3, 170-225 mm SL), 07° 11'N, 52° 56'W, 275 fm, 10 XI 1957. USNM 304720 (1, 140 mm SL), 09° 15'N, 81° 32'W, 25 V 1962. USNM 304719 (1, 94.9 mm SL), 28° 01'N, 90° 16'W, 220 fm 21 II 1962. USNM 304718 (1, 223 mm SL), 24° 28'N, 83° 24'W, 220 fm, 23 XI 1963. USNM 304716 (3, 100-215 mm SL), 23° 23'N, 86° 56'W, 8 XII 1963. USNM 304715 (1, 86.8 mm SL), 27° 44'N, 85° 09'W, 29 IX 1951. USNM 304714 (1, 109 mm SL), 13° 37'N, 81° 53'W, 250 fm, 21 XI 1968. USNM 304713 (2, 183-204 mm SL), 29° 12'N, 87° 55'W, 1 IX 1970. USNM 304712 (1, 172 mm SL), 07° 46'N, 54° 36'W, 400 fm, 7 11 1957. USNM 304710 (1, 148 mm SL), 28° 33'N, 86° 27'W, 3 XII 1962. USNM 304709 (1, 188 mm SL), 29° 07'N, 88° 09'W, 300 fm, 23 X 1962. USNM 304705 (1, 133 mm SL), 29° 00'N, 88° 35'W, 30 XI 1962. USNM 304703 (3, 168-310 mm SL), 28° 36'N, 89° 48'W, 244 fm, 21 VIII 1961. USNM 304702 (3, 88-178 mm SL), 24° 25'N, 83° 30'W, 2 XII 1963. USNM 304701 (2, 253 mm SL), 11° 49'N, 69° 24'W, 3 X 1963. USNM 304700 (1, 153 mm SL), 11° 10'N, 74° 28'W, 300 fm. 18 V 1964. USNM 304698 (1, 102 mm SL), 23° 28'N, 97° 13'W, 10 IV 1964. USNM 304697 (1, 70 mm SL), 16° 35'N, 80° 10'W, 315 fm, 18 V 1962. USNM 304693 (1, 128 mm SL), 16° 58'N, 87° 53'W, 250 fm 10 VI 1962. USNM 304692 (3, 107 mm SL + 2 bad shape), 23° 25'N, 97° 18'W, 305 fm, 2 VI 1970. USNM 304691 (1, 191 mm SL), 27° 45'N, 91° 18'W, 300 fm, 23 II 1964. USNM 304688 (1, 265 mm SL), 07° 30'N, 55° 29'W, 440 fm, 17 V 1969. USNM 304687 (3, 185-230 mm SL), 27° 15'N, 96° 00'W, 235 fm, 28 XI 1950. USNM 304686 (3, 158-212 mm SL), 09° 16'N, 81° 37'W, 280 fm, 25 V 1962. USNM 304685 (1, 155 mm SL), 11° 49'N, 69° 24'W, 3 X 1963. USNM 304681 (1, 206 mm SL), 11° 03'N, 75° 18'W, 200 fm, 2 XII 1968. USNM 304677 (1, 257 mm SL), 29° 07'N, 88° 09'W, 23 X 1962. USNM 304676 (1, 197 mm SL), 12° 06'N, 72° 55'W, 350 fm, 31 V 1964. USNM 304675 (1, 241 mm SL), 10° 10'N, 59° 54'W, 3 XI 1957. USNM 304650 (3, 74-85 mm SL), 11° 59'N, 69° 30'W, 230 fm, 27 IX 1963. USNM 304648 (5, 75-82 mm SL), 24° 22'N, 87° 47'W, 300 fm, 9 VIII 1970. USNM 304647 (1, 191 mm SL), 10° 10'N, 59° 54'W, 3 XI 1957. USNM 304636 (5, 156-197 mm SL), 24° 28'N, 83° 39'W, 26 XI 1965. USNM 304635 (3, 130-222 mm SL), 09° 13'N, 80° 44'W, 30 V 1962. USNM 304634 (1, 193 mm SL), 11° 30'N, 60° 46'W, 200 fm, 22 IX 1964. USNM 304633 (2, 183-230 mm SL), 29° 24'N, 87° 23'W, 31 VIII 1970. USNM 304630 (1, 232 mm SL), 24° 26'N, 83° 30'W, 260 fm, 26 XI 1965. USNM 304625 (3, 265-310 mm SL), 16° 51'N, 82° 14'W, 320 fm, 15 XI 1968. USNM 304622 (1, 239 mm SL), 28° 11'N, 90° 08'W, 100 fm, 20 II 1964. USNM 304620 (5, 88-277 mm SL), 24° 17'N, 87° 35'W, 300 fm, 10 VIII 1970. USNM 304619 (1, 217 mm SL), 11° 54'N, 69° 23'W, 400 fm, 3 X 1963. USNM 304617 (11, 145-230 mm SL), 09° 03'N, 81° 18'W, 300 fm, 31 V 1962. USNM 304616 (2, 266-268 mm SL), 07° 46'N, 54° 35'W, 299 fm, 10 V 1965. USNM 304615 (15, 96-277 mm SL), 16° 35'N, 80° 10'W, 315 fm, 18 V 1962. USNM 304614 (3, 222-

250 mm SL), 29° 10'N, 87° 58'W, 250 fm, 31 V 1962. USNM 304613 (20, 155-250 mm SL), 09° 00'N, 81° 23'W, 250 fm, 31 V 1962. USNM 304612 (15, 137-288 mm SL), 12° 25'N, 82° 15'W, 300 fm, 23 V 1962. USNM 304611 (3, 201-271 mm SL), 15° 45'N, 80° 45'W, 360 fm, 18 XI 1968. USNM 304610 (1, 240 mm SL), 07° 46'N, 54° 06'W, 320 fm, 25 XI 1969. USNM 304609 (8, 142-226 mm SL), 11° 12'N, 74° 21'W, 240 fm, 3 XII 1968. USNM 304576 (1, 93.5 mm SL), 30° 05'N, 87° 40'W, 18 XI 1963. USNM 304575 (3, 75-78 mm SL), 13° 39'N, 81° 52'W, 275 fm, 13 IX 1957. USNM 304573 (1, 106 mm SL), 28° 17'N, 86° 21'W, 20 VI 1969. USNM 304567 (5, 81-208 mm SL), 12° 01'N, 61° 53'W, 210 fm 26 IX 1964. USNM 304566 (2, 180-235 mm SL), 11° 53'N, 69° 25'W, 350 fm, 3 X 1963. USNM 304565 (1, 233 mm SL), 14° 23'N, 81° 45'W, 250 fm, 5 VI 1962. USNM 304564 (10, 113-186), 14° 10'N, 81° 55'W, 240 fm, 21 V 1962. USNM 304552 (4, 201-275 mm SL), 11° 40'N, 62° 33'W, 320 fm, 24 IX 1964. USNM 304550 (4, 230-242 mm SL), 18° 56'N, 94° 05'W, 7 VI 1970. USNM 304548 (13, 14-144 mm SL), 29° 59'N, 80° 08'W, 215 fm, 9 II 1965. USNM 304547 (5, 120-240 mm SL), 12° 24'N, 82° 24'W, 335 fm, 22 XI 1968. USNM 304546 (8, 164-174 mm SL), 29° 07'N, 88° 09'W, 23 X 1962. USNM 304538 (14, 165-295 mm SL), 14° 10'N, 81° 50'W, 300 fm, 21 V 1962. USNM 149844 (1), 29° 03'N, 88° 16'W, 11 II 1885. USNM 45965 (2), 11° 43'N, 69° 09'W, 18 II 1884.

Laemonema gracillipes Garman, 1899

(Fig. 29)

Laemonema gracillipes Garman, 1899: 186-188.

Laemonema gracillipes: Shmidt,1950: 44. Rass,1954: 8. Parin,1984: 57. Markle and Meléndez,1989: 875. Cohen et al., 1990:361.

Diagnosis: Head length 26.0-29.2 % SL; body depth at first anal ray 14.2-19.3 % SL; second dorsal fin with 56-63 rays; scales on a straight line 150-172.

Description: Mouth broad and terminal. Maxillary 11.1-13.5 % SL, reaching posterior ending of pupil. Barbel 3.8-5.0 % SL. Snout short 6.3-7.8 % SL. Orbit diameter 7.0-8.4 % SL, greater than interorbital width 4.4-5.4 % SL. Postorbital length 13.7-14.4 % SL.

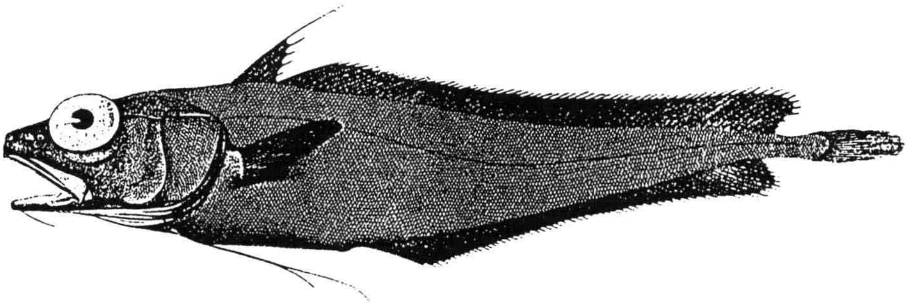


Fig. 29. Laemonema gracillipes Garman, 1899 (after Garman, 1899)

Predorsal length 26.4-29.8 % SL, dorsal origin approximately equal with end of head. Anus and anal fin closely approximate. Preanus length 36.1-46.5 % SL. Preanal fin length 38.9-50.4 % SL. Maximum body depth 19.4-20.8 % SL, occurring around middle of abdomen. Body depth at first ray of anal fin 14.2-19.3 % SL. Prepectoral length 29.6-30.8 % SL. Prepelvic length 20.6-25.4 % SL. Body decreases posteriorly to caudal peduncle; caudal peduncle depth 2.2-2.6 % SL.

First dorsal fin with six rays, its base 3.7-4.3 % SL; second ray largest, first ray embedded. Second dorsal fin with 56-63 rays (X= 59.8, mode= 61, cv= 4.0), its base 59.7-63.1 % SL, rays slowly decrease in length, but lengthen again near the end of fin, then abruptly shorten over last four or five rays. Anal fin with 55-61 rays (X= 57.3, mode= 5.8, cv = 3.8), shorter than second dorsal fin, its base 48.2-55.2 % SL; a smooth reduction in lengths of fin rays towards middle of fin. Pectoral fin ray with 21-23 rays (X= 22.2, mode= 22, cv= 3.4), its base 3.4-4.0 % SL, its length 16.7-17.6 % SL; prepectoral length 29.6-30.8 % SL. Two long pelvic fin rays 23.5-29.5 % SL; some specimens have 1-3 short and rudimentary rays; two longest pelvic fin rays reach at least 10th anal fin ray. Caudal fin rays asymmetrical, upper procurrent caudal rays 8-9 (X= 8.5, mode= 9, cv= 6.4), principal caudal rays 6, lower procurrent caudal rays 12-14 (X= 13.2, mode= 13, cv= 5.7). Total vertebrae 52-54 (X= 52.8, mode= 53, cv= 1.4), precaudal

vertebrae 15-16 (X= 15.3, mode= 15, cv= 4.4), caudal vertebrae 37-38 (X= 37.5, mode= 38, cv= 1.5). Gill rakers 6-8 + 16-21, total= 23-29. Lateral body scales 150-172, 14-15 scales above lateral line; 30-35 scales below lateral line.
Color in alcohol: According to the original description the body is brown, with a reddish tint; vertical and pectoral fin are blackish; pelvic fins are whitish. The specimens examined have been in alcohol a long time; they were completely light brown, and all fins were whitish.
Distribution: This species is distributed in the tropical eastern Pacific, near the Galápagos Islands and off Panama (Fig. 26), at 515-722 m depth.
Comments: This species is rare and poorly represented in museums. Garman (1899) considered it to be similar in shape to L. barbatulum and similar in meristic features to L. melanurum. Our data show that L. barbatulum and L. gracillipes are similar in fin ray counts, but differ in the number of lower gill rakers (10-13 in L. barbatulum vs 16-21) and scales on the lateral line (128-140 in L. barbatulum vs 155-172). Laemonema gracillipes differs from L. melanurum in having fewer pectoral fin rays (21-23 vs 25-27), more lower gill rakers (16-21 vs 12-15), no black triangular patch at the upper end of the second dorsal and anal fin, and no black rectangular patch in the caudal fin. Laemonema gracillipes differs from L. longipes in having more second dorsal fin rays (56-63 vs 49-53), more anal fin rays (55-61 vs 48-52), and more pectoral fin rays (21-23 vs 16 -18).

Laemonema gracillipes differs from L. laureysi in having more scales on a straight line (155-172 vs 120-140), more scales above the lateral line (14-15 vs 10-13), and more scales below the lateral line (30-35 vs 22). Laemonema gracillipes differs from L. yarrelli in having more scales on a straight line (155-172 vs 100-111), more scales above the lateral line (14-15 vs 8-9), and more scales below the lateral line (30-35 vs 18-23).

Material examined: MCZ 28609 (1, 169 mm SL), syntype, 00° 19'N, 90° 34'W, 331 fms, 4 VIII 1981. MCZ 67155 (1, 83 mm SL), syntype, 07° 32'N, 79° 16'W, 286 fms, 3 VIII 1891. CAS-SU 25629 (1, 221 mm SL), 00° 37'N, 81° 00'W, 401 fms, 2 III 1988. USNM 135362 (3, 187-213 mm SL), 00° 37'S, 81° 00'W, 401 fm, 2 III 1888 (one specimen cleared and stained).

Laemonema n.sp.i

(Fig. 30)

Diagnosis: Body depth 23.9-24.2 % SL, slender, covered by small, deciduous scales; pelvic fin rays long, 49.2-63.6 % SL, reaching posteriorly to mid-length of anal fin; pectoral fin with 27 rays.

Description: Head 24.4-27.4 % SL, mouth subterminal. Snout short, 7.3-8.3 % SL. Maxillary with an external row of conspicuous canine-like teeth, and two or three rows of small villiform teeth. Dentary with two rows of canine-like teeth, external ones larger than internal teeth. Teeth on vomer canine-like, in a rounded patch. Barbel on chin, 4.5-5.9 % SL, smaller than or almost equal to orbit diameter. Orbit diameter large, 5.3-5.6 % SL, at least five times into

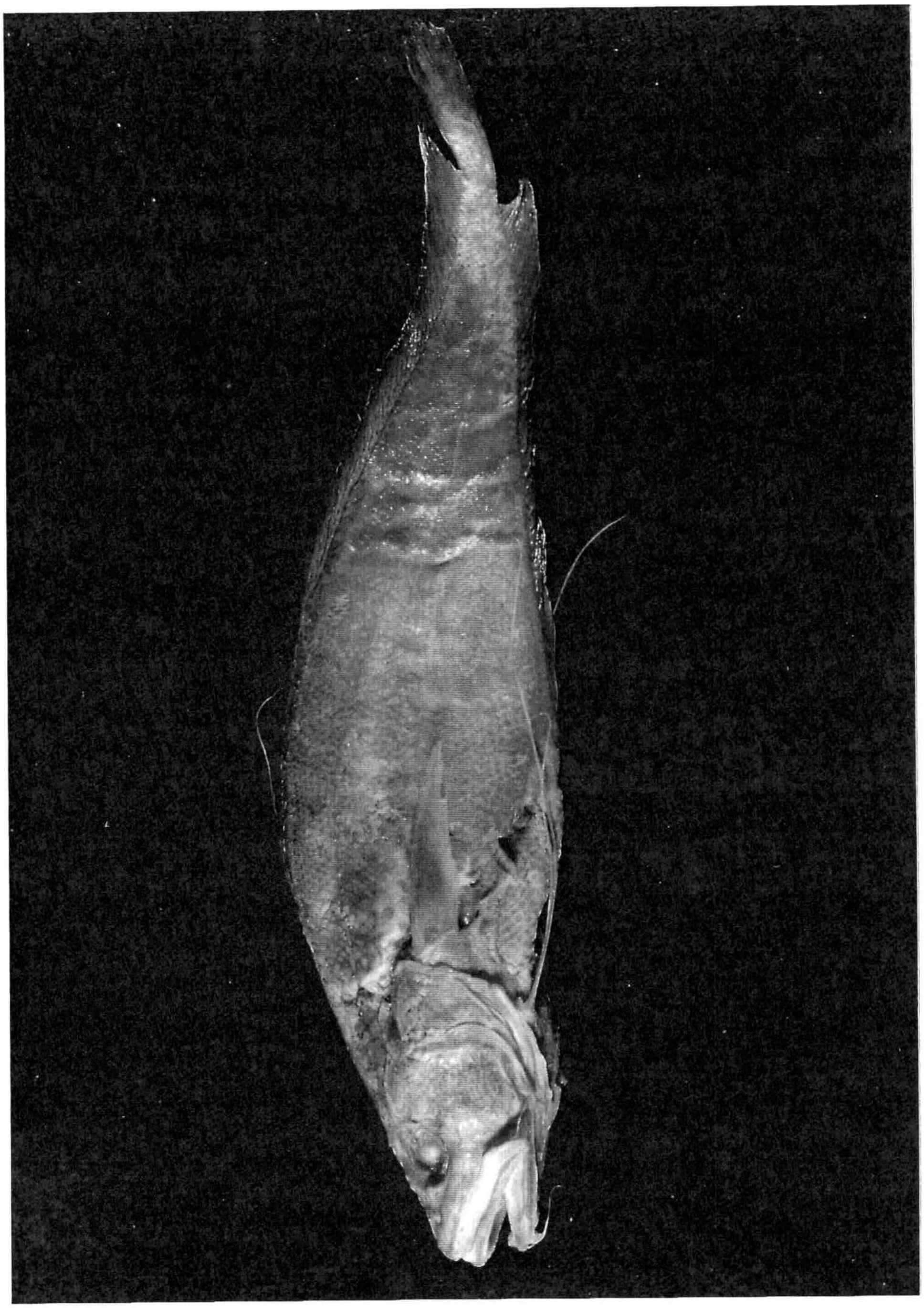


Fig. 30. Laemonema n.sp. i Holotype
RUSI 8549, male, (254 mm SL)

head length. Interorbital width short, 4.6-4.9 % SL, 5.5 times in head length, almost equal to, or a bit shorter than, orbit diameter. Maxillary 12.8-13.5 % SL, ending at about same height as posterior end of pupil. Opercle bone ending in a thin spine on its upper portion. Postorbital length 12.5-14.1 % SL.

Greatest depth of body around area of anus, 23.9-24.2 % SL. Depth at first anal ray 23.2-24.0 % SL. Anus and anal fin separated by a short distance, almost equal to height of caudal peduncle. Preanus length 39.8 % SL. Preanal fin length 43.1 % SL. Predorsal length 30.2-31.5 % SL. Depth at anus 23.1-23.6 % SL. Caudal peduncle depth 3.0-3.1 % SL.

First dorsal fin with 6 rays, base short, 4.2-4.4 % SL; first ray included in skin; second ray longest 16.9-25.2 % SL; remaining rays gradually decrease in length. Second dorsal fin with 57-58 rays, base large, 59.3-60.5 % SL, ray lengths gradually decrease from beginning to middle of fin, then increase to end of fin. Anal fin rays 54-55, shorter than second dorsal fin; base length 49.6-54.2 % SL. Pectoral fin ray with 27 rays, prepectoral length 27.6-28.0 % SL, its base 4.0-4.2 % SL. Pelvic fin with two elongated rays, their length 49.2-63.6 % SL, reaching middle of anal fin in well-preserved specimens. Caudal fin asymmetrical, 11-13 lower procurrent caudal fin rays (X= 12), upper procurrent caudal fin rays 8, principal caudal rays 6. Total vertebrae 49-51, precaudal vertebrae 14, caudal vertebrae 35-37. Gill rakers 4-5 + 12-13, total= 16-17. Lateral line not well defined, scale count on a straight line, about 126-125. Scales above lateral line 10-11, scales below lateral line 23-24.

Color in alcohol: Body light brown, vertical fins with blackish margin and whitish tips on rays of second dorsal and anal fins, and most of extension of caudal fin. Pectoral fin dark brown, with light brown edges. Pelvic fins light brown to whitish. Mouth and gill chamber light brown.

Distribution: _Laemonema_ n.sp. i has been found only off Reunion and Mauritius Island (Mascarene Island) in the Indian Ocean (Fig. 31), at 300-400m depth.

Comments: This species is distinctive among species of _Laemonema_ because of its long pelvic fins. With _L_. _robustum_ it shares similar morphometric and meristic characters, gas bladder shape, and a groove in struts 2 and 3 of the third pharyngobranchial. _Laemonema_ n. sp. i differs from _L_. _robustum_ in having fewer upper procurrent caudal fin rays (8 vs 10-12), fewer scales above lateral line (10-11 vs 14-19), and fewer scales below lateral line (23-24 vs 39-47). _Laemonema_ n.sp. i differs from _L_. _melanurum_ in having more total vertebrae (53-57 vs 49-51), fewer scales on a straight line (125-126 vs 145-166), fewer scales above the lateral line (10-11 vs 18), fewer scales below the lateral line (23-24 vs 35-36), and in lacking the special color pattern of the second dorsal, anal and caudal fin _L_. _melanurum_. _Laemonema_ n. sp i differs from _L_. _rhodochir_ in having fewer second dorsal fin rays (57-58 vs 61-66), fewer anal fin rays (54-55 vs 58-63), and more pectoral fin rays (27 vs 22-24).

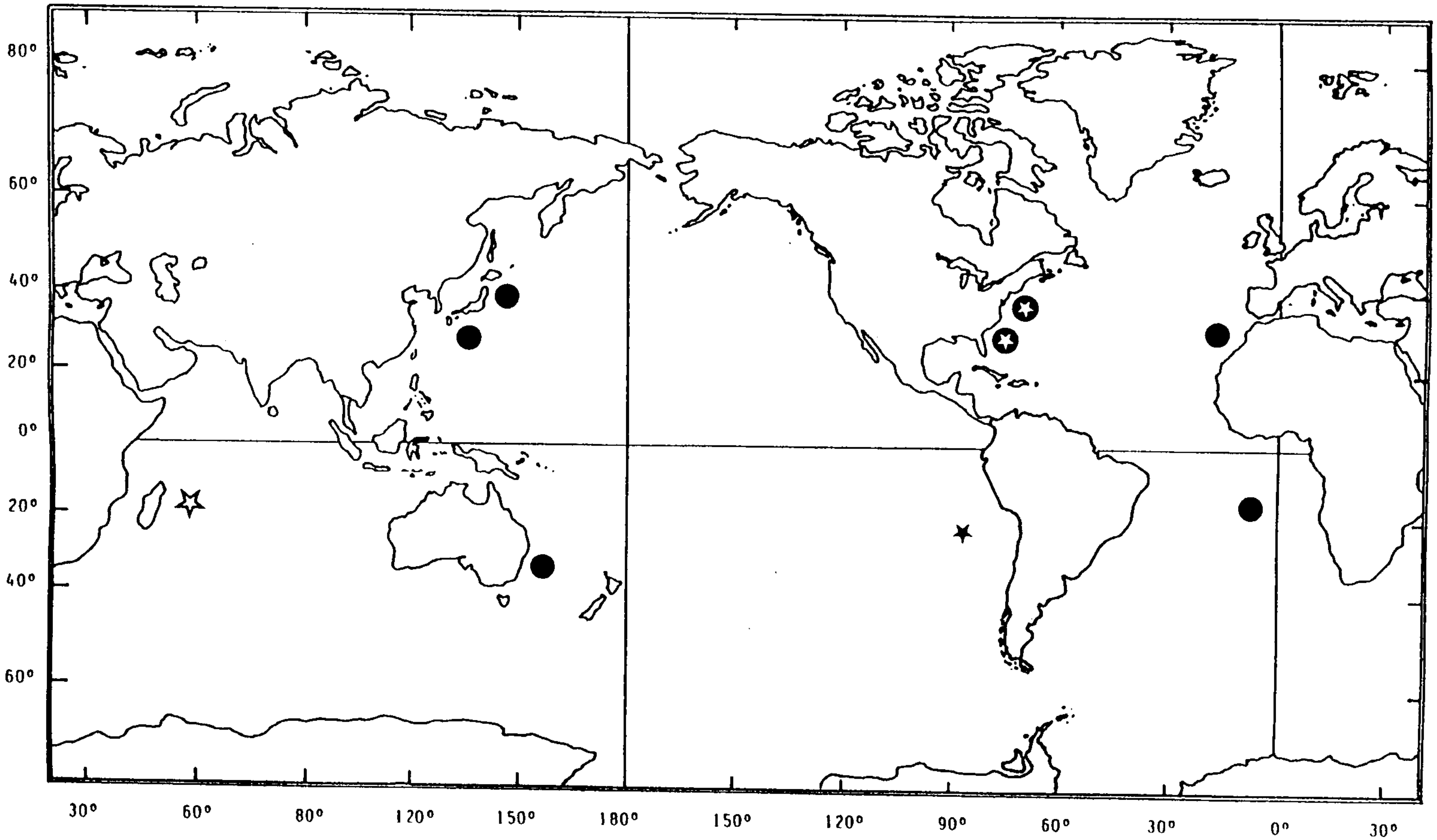


Fig. 31. Distribution map of Laemonema n.sp. i (☆), Laemonema melanurum (✪), Laemonema robustum (●) and L. yuvto (✶).

Laemonema n. sp i differs from L. yuvto mainly in the lower counts of the second dorsal fin (57-58 vs 62), and the lower counts of rays in the pectoral fin (27 vs 31).

Material examined: Holotype :RUSI 8549, 254 mm SL, male, Mauritius Island, 300-400 m caught in trap. 1978, coll: Baissac. Paratypes: RUSI 1423, +/- 230 mm SL, tail broken. Reunion Island, June 1966, coll: Gueze (cleared and stained). MNHN 1966-848. 236 mm SL, Reunion Island.

Laemonema laureysi Poll, 1953

(Fig. 32)

Laemonema laureysi Poll,1953: 197-200.

Laemonema laureysi: Parin,1984: 57. Cohen, 1986:327. Lloris, 1986: 252-254. Cohen,1990:552, Cohen et al., 1990: 361.

Diagnosis: Second dorsal fin with 63-72 rays, modally 66 rays; height of first dorsal fin 11.9-29.2 % SL, average 22.4 % SL; body slender, depth 11.9-22.4 % SL, covered with deciduous scales.

Description: Head short 21.9-25.1 % SL. Mouth broad, maxillary 10.2-12.5 % SL, reaching middle of pupil, with two outer rows of strong caninelike teeth and four or more rows of small teeth. Vomer rounded, with teeth. Dentary with same type of teeth as in maxillary. Barbel 2.7-4.7 % SL, always present. Snout short, 5.4-7.4 % SL. Orbit diameter 6.3-8.8 % SL, almost double interorbital width, 3.2-4.6 % SL. Postorbital length 9.5-11.8 % SL.

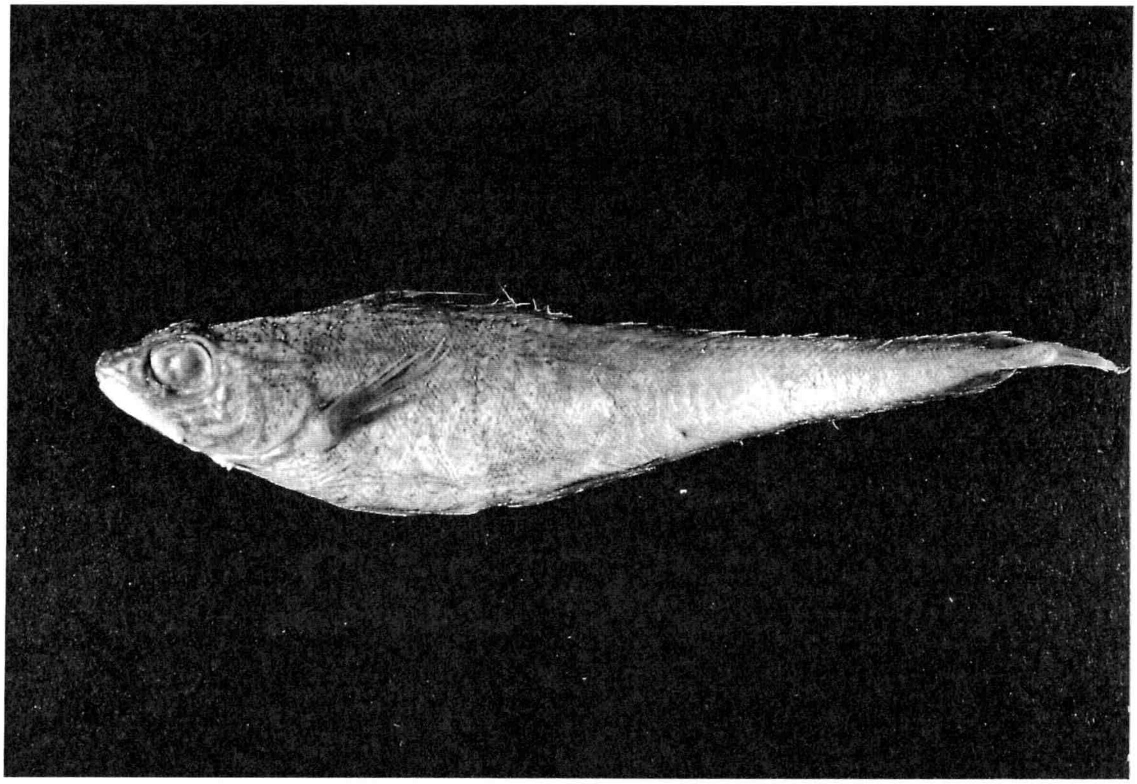


Fig. 32. Laemonema laureysi Poll, 1953 Paratype
IRSB 175 (230 mm SL)

Predorsal length 22.7 -27.5 % SL. Anus and anal fin not separated; preanus length 34.4-43.9 % SL; preanal length 36.9-46.2 % SL. Maximum depth of body 11.9-22.4 % SL. Depth at first anal ray 13.1-23.5 % SL. Prepectoral length 15.9-26.5 % SL. Prepelvic length 14.9-25.5 % SL. Caudal peduncle narrow, its depth 1.9-2.8 % SL.

First dorsal fin with 5-7 rays (X= 5.9, mode= 6, cv= 3.8), its base 2.3-5.0 % SL; first ray embedded; second ray is longest, 11.9-29.2 % SL (X= 22.4, mode= 23.4, cv= 14.1). Second dorsal fin with 63-72 rays (X= 66.2, mode= 66, cv= 2.6), its base 63.3-72.0 % SL. Anal fin with 60-69 rays (X=64.2, mode=64, cv=3.1), its base 50.0-58.1 % SL. Pectoral fin with 19 -23 rays (X= 20.8, mode= 21, cv= 4.0), its base 2.7-3.9 % SL, its length 12.7-18.6 % SL. Pelvic fin with two long rays, which reach and extend beyond anus; length 23.1-42.5 % SL. Caudal fin asymmetrical, upper procurrent rays 7-10 (X= 8.5, mode= 9, cv= 7.5), principal caudal rays 6, lower procurrent rays 10-15 (X= 12.8, mode= 13, cv= 8.2). Total vertebrae 53-58 (X=55.3, mode= 55, cv= 1.7), precaudal vertebrae 14-17 (X= 15.3, mode= 15, cv= 3.7), caudal vertebrae 38-43 (X= 39.9, mode= 40, cv= 2.3). Gill rakers 5-8 (X= 7.3, mode= 7, cv= 8.0) + 16-21 (X= 18.4, mode= 19, cv= 5.2), total= 22-29. Scales on a straight line 120-140, scales above lateral line 10-13 (X= 10.7, mode= 10, cv= 9.8). Scales below lateral line 22-24 (X= 22.4, mode= 22, cv= 3.5).

Color in alcohol: Body mainly light gray, with area near viscera darker. Areas above head and near vertical fins dark. Vertical fins and caudal fin dark; pectoral and pelvic fin whitish.

Distribution: This is a benthopelagic species of the upper slope at depths of 220-510m (Cohen et al. 1990), found from the Mauritania upwelling area to Namibia in the subtropical and tropical eastern Atlantic (Fig. 26). Our data expand the depth range to 618m.

Comments: Laemonema laureysi is one of the most abundant Laemonema in museums, and the paratypic series is quite large. The species is closely related to the newly described L. n.sp. g (Table 6). A t-test comparison of second dorsal and anal fin rays of L. laureysi and L. n.sp. g showed a D2 t-test value of 273.435 (P= 0.00); for anal fin rays the t-test value was 239.908 (P=0.00). Even though counts for the meristic characters D2, A, PC, CV and TV, for L. laureysi and L. n.sp. g span a broad range (Table 6), the meristics counts in L. laureysi tend to be concentrated within a smaller range than in L. n.sp. g. This difference could be explained by some environmental characteristic, like temperature. Other differences between both species were discussed in the description of L. n.sp. g.

Laemonema laureysi differs from L. longipes in having more second dorsal fin rays (63-72 vs 49-53), more anal fin rays (54-55 vs 48-52), and a round vomer compared to a v-shaped vomer in L. longipes. Laemonema laureysi differs from

Table 6.- Comparison between selected meristic characters of <u>Laemonema</u> <u>laureysi</u> and <u>L</u>. n. sp. g

	D2											A											
	63	64	65	66	67	68	69	70	71	72	73	60	61	62	63	64	65	66	67	68	69	70	71
<u>L</u>. <u>laureysi</u>	2	7	9	17	11	4	4	1		1		3	2	6	7	12	12	7	5	1	1		
<u>L</u>. n. sp. g				1	2	6	6	14	3	3	3						4	3	8	6	8	6	1

	PC				CV						TV						
	14	15	16	17	38	39	40	41	42	43	53	54	55	56	57	58	59
<u>L</u>. <u>laureysi</u>	1	39	14	2	4	10	30	9	1	1	1	9	23	18	2	1	
<u>L</u>. n. sp. g		1	27	9		1	2	19	7	5				3	13	12	6

L. yarrelli in having more second dorsal fin rays (63-72 vs 58 -62), more scales on a straight line (120-140 vs 100-111), and in lacking the coloration pattern of the vertical fins in L. yarrelli.

Material examined: IRSB 175 (11, 146-238 mm SL), paratypes 07° 16'S, 12° 02'E, 380-420 m, 1 X 1948 (one paratype cleared and stained). LACM uncat. (1, 183 mm SL), R/V Dr. Nansen off Angola. MMF 3316 (1, 258 mm SL), Angola, II 1962. MNHN 1987-1027 (4, 158-181 mm SL), 14° 01'N, 17° 31'W, 330 m, 25 V 1979. MNHN 1967-797 (7, 84-224 mm SL), off Pointe Noire. MCZ 56974 (13), 21° 21'N, 17° 37'W, 400 m, 23 V 1974. MCZ 86749 (2, 98.2-170 mm SL), 21° 21'N, 17° 37'W, 400 m, 23 V 1974. MSU uncat. (1, 230 mm SL), 10° 54'S, 13°22'E, 520 m, 24 II 1976. MSU uncat. (5 (out of 10), 108-203 mm SL), ca. 18-19°S , 11-11°30'E, ca. 300 m. off Namibia, 27 I 1988. MSU 11423 (2,. 205-212 mm SL), 17°48'S, 11°36'E, 21 V 1965. MSU uncat. (2, 194-198 mm SL), 03°17'S, 09°33'E, 500 m, 19 IV 1976. PPSIO uncat. (7 out of 9, 130-198 mm SL), 18°50'N 16°50'W, 450-470 m. PPSIO uncat. (1, 198 mm SL), 7°43'N, 16°41'W. PPSIO uncut (2, 115-171 mm SL), 04°50'N, 05°24'W, 300 m 27 I 1967. PPSIO uncat. (2, 115-171 mm SL), 04°50'N, 05°24'W, 300 m 27 I 1967. UF 47559 (5, 104-236 mm SL), 01° 57'S, 08° 46'W, 220 fms, 4 IX 1963. UF 47560 (1, 245 mm SL), off NW coast of Africa. USNM 300892 (3, 178-197 mm SL), 01° 28'S, 08° 24'W, 300 m, 03 IX 1963. USNM 301096 (5, 197-242 mm SL), 09° 10'N, 15° 39'W, 600-610 m, 28 XI 1963. USNM 301096 (5, 197-242 mm SL), 09° 10'N, 15° 39'W, 600-610 m, 28 XI 1963.

Other material of L. laureysi examined but not included in the analysis: MNHN 1886-556 (1, not good shape), st CXI, R/V Talisman, 580 m, 1883. MNHN 1886-563 (1)(same as MNHN 1886-556). MNHN 1886-564 (1)(same as MNHN 1886-556). MNHN 1886-565 (1)(same as MNHN 1886-556). MNHN 1886-557 (1, not good shape), st CXIIIA, R/V Talisman, 618 m, 1883. MNHN 1886-558 (1)(st CXIIIA, R/V Talisman, 618 m, 1883). MNHN 1886-558 (1)(st CXIIIA, R/V Talisman, 618 m, 1883). USNM 304626 (18), 17° 23 S, 11° 20'E, 366 m, 24 III 1968. USNM 304735 (1, 226 mm SL), 05° 38'N, 10° 25'W, 25 IV 1964. USNM 304734 (2, 96-124 mm SL), 08° 57'N, 14° 59'W, 395 m, 27 XI 1963. USNM 304571 (1, 108 mm SL), 05° 23'S, 11° 34'E, 400 m, 24 V 1964. USNM 304568 (5, 165-228 mm SL), (same as USNM 304571) USNM 304559 (2, 218-238 mm SL), 03° 05'S, 09° 15'E, 604 m, 6 IX 1963. USNM 304554 (1, 220 mm SL), 08° 57'N, 14° 59'W, 395 m, 27 XI 1963. USNM 304549 (4, 197-269 mm SL), 02° 30'S, 08° 52'E, 5 IX 1963. USNM 304543 (10, 176-287 mm SL), 04° 36'N, 09° 15'W, 400 m, 2 XI 1963. USNM 304542 (5, 187-275 mm SL), 04° 06'S, 10° 23'E, 400 m, 8 IX 1963. USNM 304541 (4, 202-

250 mm SL), 05° 38'N, 10° 26'W, 600 m, 6 XI 1963. USNM 304540 (4, 141-251 mm SL), 05° 59'N, 03° 34'W, 400 m, 7 X 1963.

Laemonema longipes (Shmidt, 1938)

(Fig. 33)

Laemonema longipes Shmidt,1938: 655.

Laemonema longipes: Okamura,1984:91, Cohen et al. 1990.

Podonema longipes: Rass,1954: 2.

Podonematichthys longipes: Whitley,1965: 25.

Laemonema morosum Matsubara,1938: 61-62.

Diagnosis: Body long, slender, covered by small, deciduous scales; second dorsal fin with 49-53 rays; vomer with teeth in a V-shape; no barbel on chin.

Description: Head 20.2-24.6 % SL; mouth subterminal. Snout large, 6.3-7.5 % SL. Maxillary with an external row of conspicuous canine-like teeth, with two or three inner rows of small villiform teeth. Dentary with two rows of canine-like teeth, external ones largest, internal teeth smaller. Teeth on vomer canine-like, in a v-shaped patch. No barbel on chin. Orbit diameter 3.5-5.6 % SL, almost 5.0 in head length. Interorbital width broad, 3 in head length, and almost 1.5 in orbit diameter, 5.9-7.3 % SL. Maxillary 9.0-11.8 % SL, ending at about same height as the posterior end of pupil. Opercle bone ending in a spine in its upper portion. Postorbital length 10.8-13.0 % SL.

Greatest depth of body around area of anus, 12.6-18.5 % SL. Body depth at first anal ray 11.8-15.5 % SL. Anus and

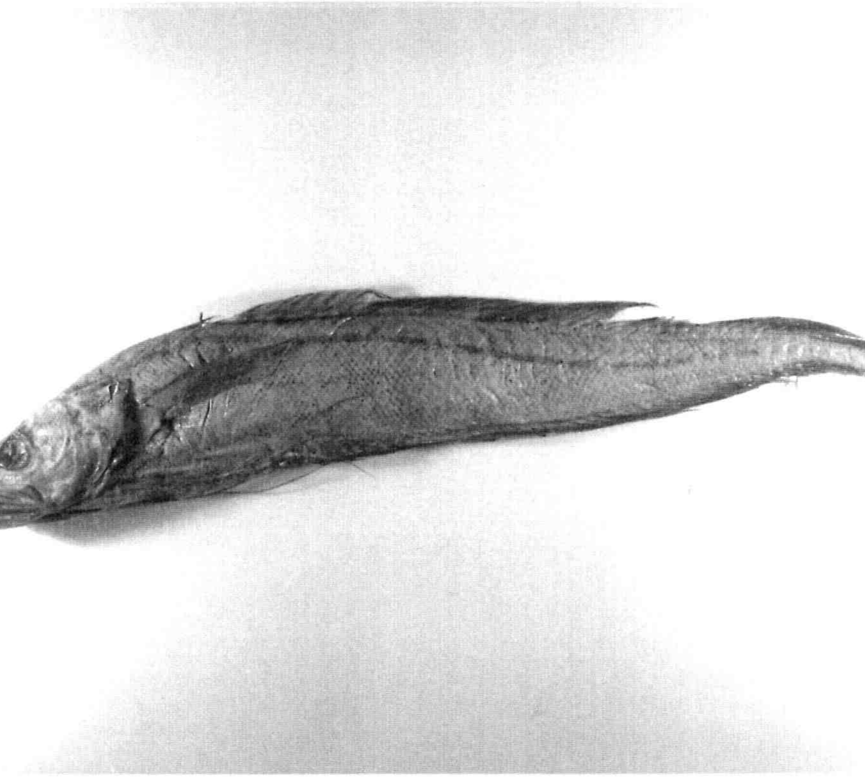


Fig. 33. Laemonema longipes Shmidt, 1939
HUMZ 81033 (475 mm SL)

anal fin separated by a short distance, shorter than height of caudal peduncle. Preanus length 32.5-36.4 % SL. Preanal fin length 33.9-38.0 % SL. Predorsal length 22.3-27.0 % SL. Depth at anus 11.8-15.4 % SL. Caudal peduncle depth 1.4-2.6 % SL.

First dorsal fin with 6 rays, short base 4.7-7.1 % SL; first ray not embedded, second ray longest, 8.4-12.6 % SL, remaining rays gradually decrease in length. Second dorsal fin with 49-53 rays (X= 50.6, mode= 51, cv= 2.3), base long 61.6-69.3 % SL, ray lengths gradually decrease from beginning to end. Anal fin with 48-52 rays (X = 49.7, mode = 49, cv= 2.8), base lightly shorter than second dorsal fin 58.6-62.6 % SL. Pectoral fin ray with 16-18 rays (X= 17.1, mode = 17,cv= 3.7), its base 2.5-3.2 % SL; prepectoral length 21.0-25.6 % SL. Pelvic fin with two elongated rays, its length 26.4-42.3 % SL, reaching anus. Caudal fin asymmetrical, 9-11 lower procurrent rays (X= 10, mode= 10, cv= 4.7), upper procurrent rays 7-8 (X= 7.8, mode= 8, cv= 5.4), principal rays 5-6 (X= 5.9, mode= 6, cv= 5.4). Total vertebrae 49-52 (X= 50.4, mode= 49, cv= 2.5), precaudal vertebrae 14-16 (X= 15.1, mode= 15, cv= 3.8), caudal vertebrae 34-37 (X= 35.3, mode= 35, cv= 3.0). Gill rakers 7-8 + 18-20, total= 26-28. Lateral line not well defined, count on straight line about 110-144 scales. Scales above lateral line 10-11 (X= 10.2, mode= 10, cv= 4.0), below lateral line 20-25 (X= 22.5, mode= 25, cv= 15.7).

Color in alcohol: Body grey; second dorsal fin, caudal and anal fins with blackish tips.

Distribution: Laemonema longipes is distributed in the western North Pacific, from off Owase, Japan to the eastern Bering Sea (Yabe et al. 1981; Cohen et al. 1990) (Fig. 23). Cohen et al. (1990), considered this fish as benthopelagic on the continental slope from 455 to 1400 m depth. Pautov (1980) indicated 1900m depth. It is locally abundant in the Sea of Okhotsk (Shmidt,1950) and off Japan where commercial concentrations occur at 200-800 m (Pautov 1980). It is the best studied Laemonema with several recent Japanese and Russian articles on its biology and fishery.

Comments: Both Laemonema longipes and L. morosum were described in the same year, but Shmidt's paper appeared in June 1938, while Matsubara's paper was published in July 1938. Because of the Rule of Priority, the valid name for this species is L. longipes, and L. morusum becomes a junior synonym. Rass (1954) erected a new genus for this species, Podonema. However, Whitley (1965) found that Podonema was preoccupied in Insecta, so he proposed a replacement name, Podonematichthys. This species is similar morphologically to some species of the gadiform family Merluccidae. It is one of the few morids considered to be a potential commercial resource (Cohen et al. 1990). Laemonema longipes differs from other Laemonema species in the absence of a barbel, in the presence of a v-shaped vomer, and in the shape of the gas bladder, with the exception of L. verecundum, which also has a v-shape vomer and approximately the same shape of gas bladder, but differs in meristic counts, mainly in counts of the first dorsal fin (6 vs 8-9).

Material examined: CAS 47657 (4, 119-141 mm SL), 52° 38'N, 172° 45'E, 412-416 m, 19 VIII 1980 (one specimen cleared and stained). HUMZ 81033 (1, 475 mm SL), off Muroran, Hokkaido, 14 VII 1978, Japan. HUMZ 81034 (1, 445 mm SL), (same as HUMZ 81033). HUMZ 81035 (1, 463 mm SL), (same as HUMZ 81033). PPSIO uncat. (1, 207 mm SL), Sea of Okhost, st 155. USNM 161488 (2, 375-380 mm SL), 48° 25'N, 145° 30'E, 241 fm, 28 IX 1906. USNM 149844 (5, 126-133 mm SL), 26 IX 1906, Saghalin Island. USNM 150362 (1, 488 mm SL), 30 IV 1949, Muroran, Hokkaido, Japan. USNM 220877 (1, 215 mm SL), 56° 00'N, 169° 14'W, 595-610 m, 18 VI 1979.

Laemonema melanurum Goode and Bean, 1896

(Fig. 34)

Laemonema melanurum Goode and Bean, 1896:363-364.

Laemonema melanurum: Holt and Byrne, 1908: 87. Matsubara, 1938:62. Taki,1953: 208. Rass,1954:8. Lindberg and Legeza, 1965: 230. Parin,1984:57. Cohen et al. 1990: 361.

Diagnosis: Body slightly broad, covered by small, deciduous scales; first dorsal fin with seven rays; pectoral fin with 25 -27 rays; anal fin with a conspicuous depression at middle-length; posterior end of dorsal and anal fins have a black triangle, and end of caudal fin with a black vertical band.

Description: Head length 24.4-33.2 % SL; maxillary 11.2-15.9 % SL, reaching middle of pupil, with outer row of strong canine-like teeth, followed by three or more irregularly distributed, small inner canine-like teeth; toothless space at symphysis. Vomer with caniniform teeth in rounded patch.

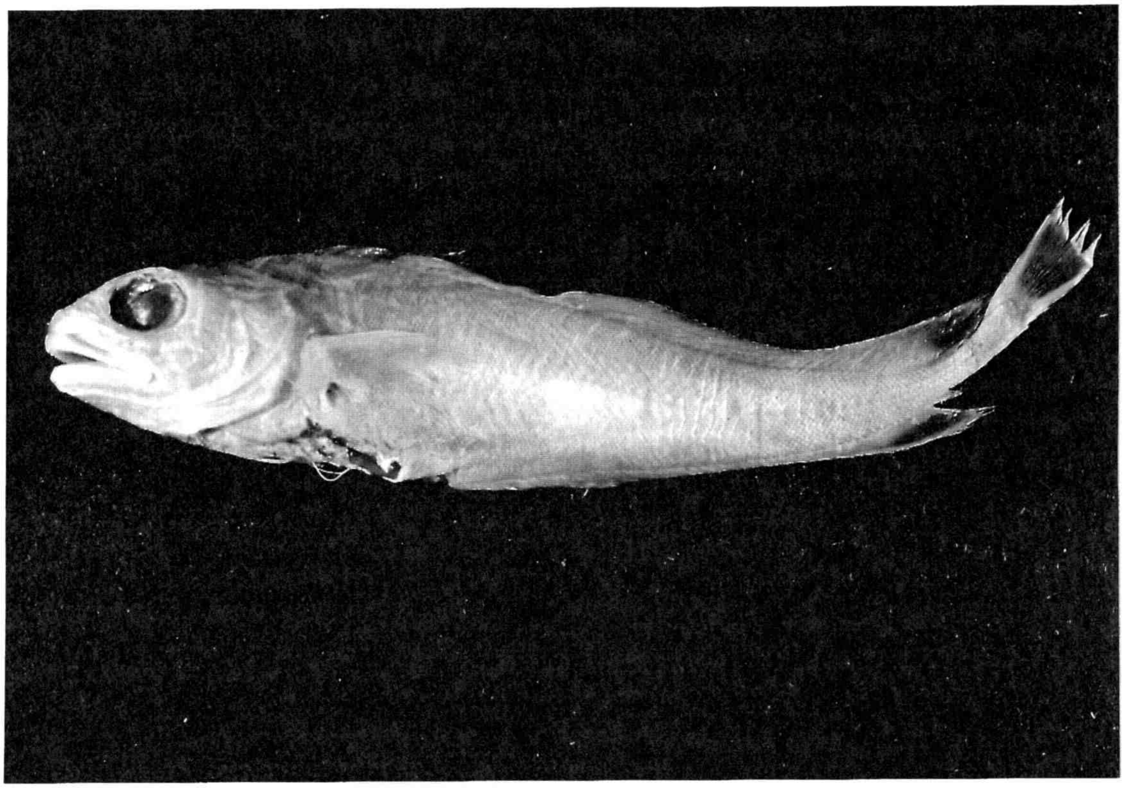


Fig. 34. Laemonema melanurum Goode and Bean, 1896
USNM 304411 (181 mm SL)

Dentary with teeth arrangement similar to that of maxilla but without toothless space. Orbit diameter 7.1-11.1 % SL, larger than interorbital width, 4.5-9.7 % SL. Two nostrils, both near eyes, the farthest from eye with a siphon like structure, nearest with an elevated membrane. Snout short, 5.6-7.9 % SL. Barbel always present, 1.8-6.4 % SL. Postorbital length 10.7-13.0 % SL. Opercle with a flat spine.

Predorsal length 24.4-39.2 % SL, slightly greater than head length. Prepectoral length, 23.8-29.7 % SL; pectoral origin about at the same vertical as origin of first dorsal fin. Prepelvic length 17.3-23.8 % SL. No separation between anus and anal fin. Preanus length 38.0-52.0 % SL; preanal length 41.0-55.0 % SL. Maximum depth below first dorsal fin 19.0-33.0 % SL. Depth at anus 12.4-50.8 % SL. Body continuously decreasing in size to caudal peduncle, which is short 1.8-3.3 % SL.

First dorsal fin with seven rays, its base short, 4.7-10.9 % SL, second ray longest 17.4-25.9 % SL. Second dorsal fin with 53-61 rays (X= 56.9, mode= 56, cv= 4.3), its base 51.2-64.1 % SL. Anal fin with 52-59 rays (X= 55.6, mode= 54, cv= 3.9), its base 42.5-52.4 % SL. Pectoral fin with 25-27 rays (X= 25.9, mode= 25, cv= 3.5), its base 3.9-7.7 % SL, its length 15.8-25.0 % SL. Pelvic fin with two rays, its length 17.4-30.8 % SL. Caudal fin asymmetrical, upper procurrent rays 7-10 (X= 9.0, mode= 9, cv= 10.4), principal rays six, lower procurrent ray 11-15 (X= 12.9, mode= 13, cv=

8.8). Total vertebrae 53-57 (X= 54.5, mode= 55, cv= 2.2), precaudal vertebrae 15-16 (X= 15.1, mode= 15, cv= 1.9), caudal vertebrae 38-42 (X= 39.4, mode= 39, cv= 3.0). Gill rakers 4-6 (X= 5.1, mode= 5, cv =11.7) + 12-15 (X= 12.7, mode= 12, cv= 8.2), total= 16-21. Scales on a straight line 145-166, scales above lateral line 18, scales below 35-36 (X= 35.7, mode= 36, cv= 1.6).

Color in alcohol: Body light brown, with a prominent black patch on most of caudal fin; black patches present also at end of second dorsal and anal fins, both have thin black line along the margins.

Distribution: This species is restricted to the western North Atlantic Ocean at depths of 445-634 m (Fig. 31).

Comments: Adult specimens are not well represented in museums and we examined only 6 adults. As discussed above, *L. melanurum* seems most similar to *L. gracillipes*. Postlarval and juvenile specimens, the "*Svetovidovia*" of Fahay and Markle (1984), are more available. The postlarvae and juveniles have seven to ten pelvic rays, which are reduced/reabsorbed (Fig. 35) leaving only two visible pelvic rays (Table 7) in adults.

This species is distinctive because of the color pattern of vertical fins: a black triangular patch on the upper end of the second dorsal and anal fin, and a rectangular black patch on the caudal fin. *Laemonema melanurum* differs from *L. robustum* in having more total vertebrae (53-57 vs 47 -52) and fewer scales below the

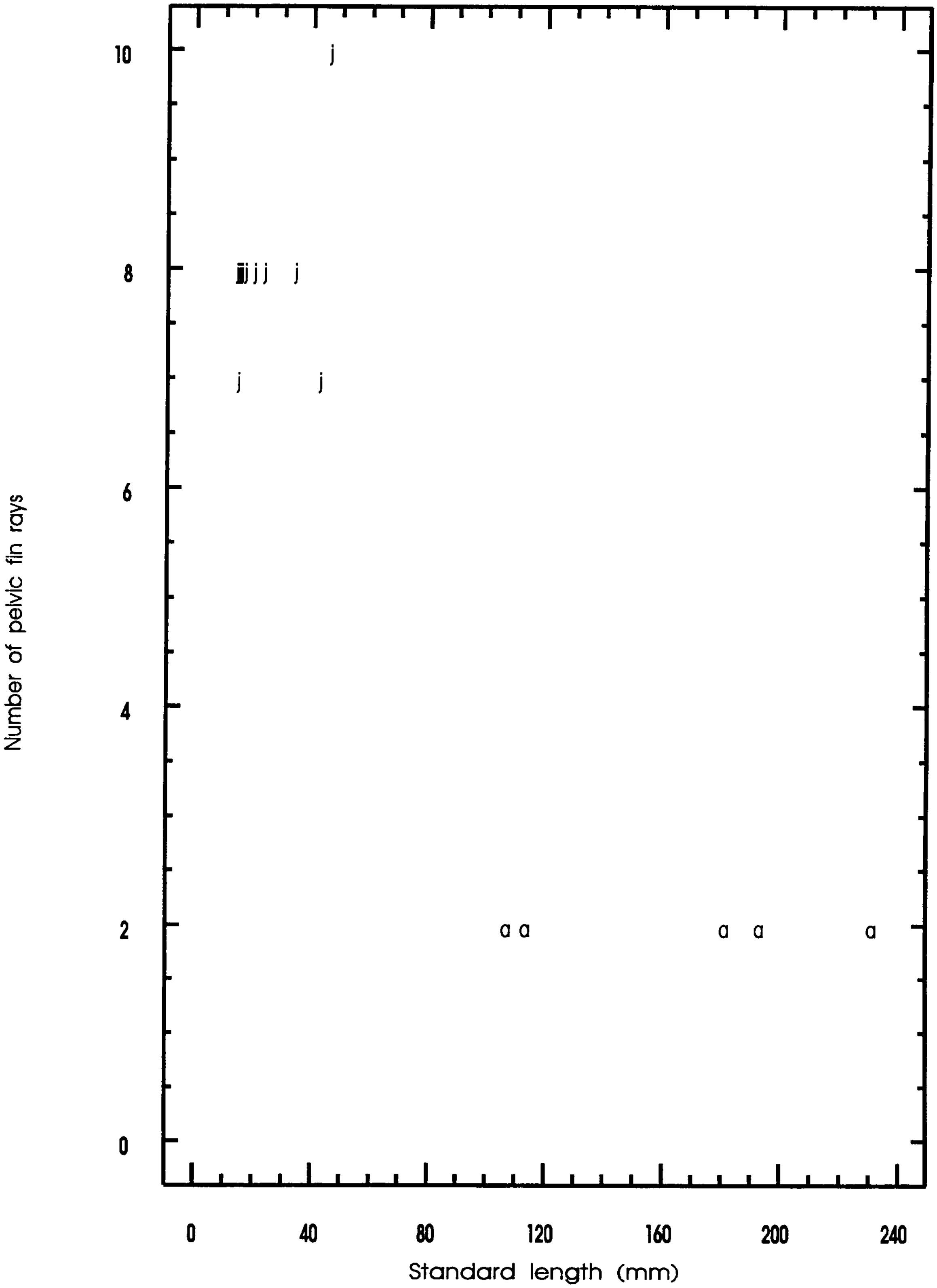


Fig. 35. Number of pelvic fin rays vs Standard length for *L. melanurum* (a= adults, j= juveniles).

Table 7.- Comparison between selected meristics characters of postlarval and adults of *Laemonema melanurum*

	range (mm)	D2									A							
		53	54	55	56	57	58	59	60	61	52	53	54	55	56	57	58	59
L. melanurum	>100			1	1	1	2		1				1	1	1	1	2	
L. melanurum	< 50	1	2	2	2	1		3		1	1	1	4	1		1	2	1

	range (mm)	PCV		CV					TV				
		15	16	38	39	40	41	42	53	54	55	56	57
L. melanurum	>100	6	1	1	4				1	3	1		
L. melanurum	< 50	6		1		3		1	1		3		1

	range (mm)	LGR				UGR			UPC				LPC				
		12	13	14	15	4	5	6	7	8	9	10	11	12	13	14	15
L. melanurum	>100	2	2	1	1		2	4			3	2			3	2	
L. melanurum	< 50	8	2		1	2	9		1	1	2	2	1	3	1		1

lateral line (35-36 vs 39-47). Laemonema melanurum differs from L. rhodochir in having more pectoral fin rays (25-27 vs 22-24), more scales on a straight line (145-166 vs 105-130),and more scales below the lateral line (35-36 vs 21). Laemonema melanurum differs from L. yuvto in having fewer pectoral fin rays (25-27 vs 31), more caudal vertebrae (53-57 vs 51), and more scales on a straight line (145-166 vs 135).

Description of early stages of Laemonema melanurum: A specimen of 46.4 mm SL (ARC uncat.)(HML No 29 set 26) had its stomach expanded. Pelvic rays eight, higher than in adults. Rays of pectoral fin 27, relatively shorter than in larger individuals, not reaching dorsal profile of body. Body color light brown, including caudal peduncle. Visceral area darker, same as base of dorsal and anal fins.

Individuals from 42 mm to 16 mm SL (ARC 8707565, ARC 8707593, ARC uncat., 4 specimens, and MCZ uncat.) with caudal peduncle and caudal fin unpigmented. Body pigmentation varies from mixed dark and light brown to darkest body with large melanophores in smaller individuals. At 26 mm SL, pectoral fin rays attains its greatest length, reaching dorsal contour of body. In individuals 42 mm and above, stomach exhibits "gluttonous habit" (Markle, 1989). Pelvic fin rays eight, all same size.

Smallest individual identified as L. melanurum 15.6 mm SL (ARC 8707565) and characterized by large eyes, 38.8 % HL. All fins formed, pelvic fin with 8 rays. Caudal peduncle unpigmented. Area of viscera densely pigmented. Maximum body depth located at origin of first dorsal fin, from this point body size decreases posteriorly to tail and anteriorly to head. Color of body light brown; two more-pigmented lines immediately below dorsal fin and above anal fin; head whitish except above eyes, with small melanophores arrangement in rows.

Material examined: ARC 8707565 (1, 17.1 mm SL), 41° 05'N, 66° 32'W, oblique IKMT, 19 V 1982. ARC 8707577 (1, 40.6 mm SL), 42° 06'N, 65° 05'W, oblique IKMT, 22 VI 1980. ARC 8707593 (1, 44 mm SL), 43° 22'N, 60° 32'W, oblique IKMT, 17 VI 1980. CAS-SU 9445 (1, 231 mm SL), 32° 35'N, 77° 30'W, 247 fms, 21 X 1885. USNM 38270 (1, Holotype, 320 mm SL), 30° 44'N, 79° 26'W, 1 IV 1885. USNM 38269 (1, 181 mm SL), 33° 18'N, 79° 07'W, 0-276 fm, 1 IV 1885. USNM 53058 (1, 193 mm SL), 31° 09'N, 79° 33'W, 352 fm, 5 V 1886. USNM 304411 (3, 107-181 mm SL), 31° 47'N, 78° 23 W, 630-640 m, 7 XI 1979 (one specimen cleared and stained).

Laemonema rhodochir Gilbert,1905

(Fig. 36)

Laemonema rhodochir Gilbert, 1905: 657-658.

Laemonema rhodochir: Taki,1953:8. Rass,1954:5. Parin, 1984: 56-59. Cohen et al., 1990: 361. Parin and Sazonov, 1990:8.

Laemonema palauense Okamura, 1982:136-139.

Laemonema palauense: Okamura,1984:92. Parin and Sazonov, 1990:8.

Diagnosis: Body low and slender, covered by small deciduous scales; conspicuous pores below eye; lower gill arch with 11-14 gill rakers; pectoral fin with 22-24 rays.

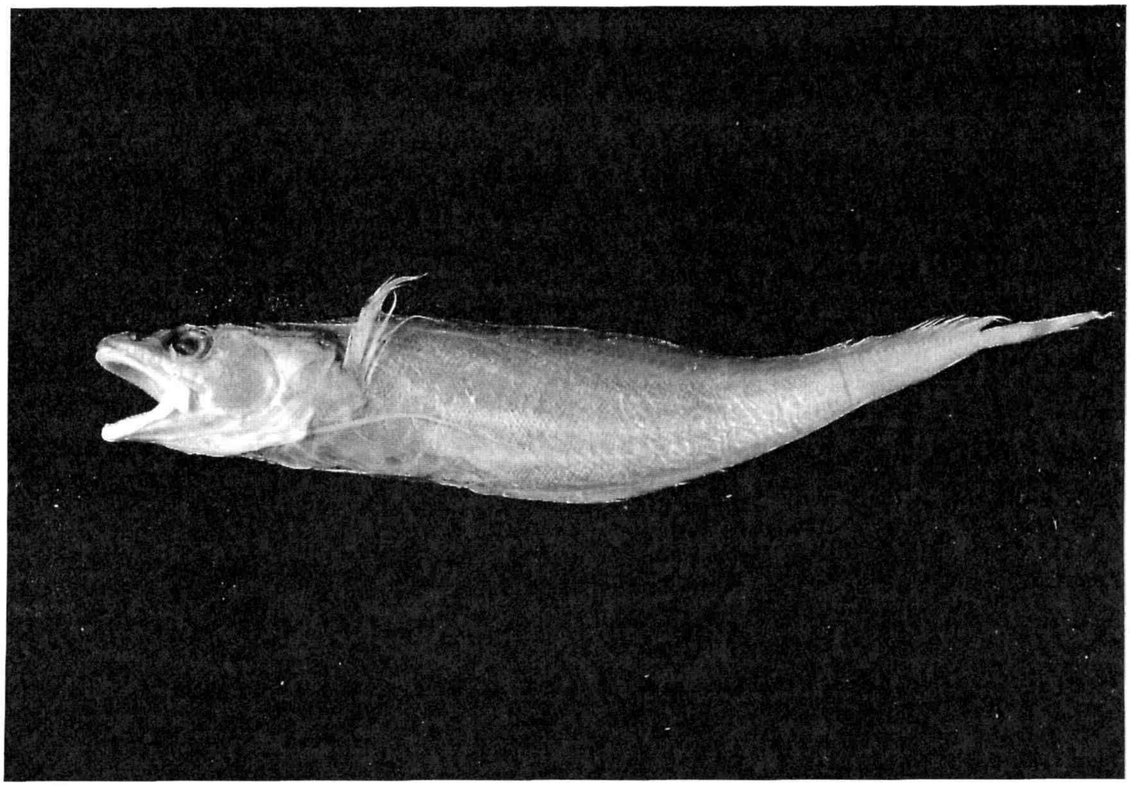


Fig. 36. Laemonema rhodochir Gilbert, 1905
PPSIO uncataloged (127 mm SL)

Description: Head length 22.2-24.9 % SL. Maxillary 9.7-11.9 % SL, reaching end of pupil, with two rows of strong caninelike teeth followed by three rows of smaller teeth. A rounded patch of caninelike teeth on vomer. Dentary with four or more rows of similar-sized caniniform teeth. Snout 6.5-7.6 % SL, without scales. Barbel 3.3-5.6 % SL, always present, longer than interorbital width. Orbit diameter 5.1-7.0 % SL, longer than interorbital width, 3.4-4.9 % SL. Superior area of orbit with two pores. Postorbital length 10.1-24.9 % SL.

Predorsal fin length 25.1-29.4 % SL. Anus and anal fin not separated. Preanal fin length 36.7-43.5 % SL. Preanus length 34.1-39.7 % SL. Prepelvic fin 17.8-23.6 % SL. Prepectoral length 23.3-27.0 % SL. Maximum depth of body below first dorsal fin 15.7-21.5 % SL. Body depth at first anal ray 15.2-19.4 % SL; body decreases posteriorly to caudal peduncle, 1.8 -3.1 % SL, which is less than length of barbel.

First dorsal fin with six rays, its base 3.1-4.7 % SL, its second ray longest, 8.3-12.6 % SL; first fin ray embedded in skin. Second dorsal fin with 61-66 rays (X= 64.4, mode= 64, cv= 2.3), its base 61.3-67.8 % SL, length of rays decrease posteriorly. Anal fin with 58-63 rays (X= 60.2, mode= 61, cv= 2.9), its length 52.5-58.5 % SL, rays shorter around middle of anal fin. Pectoral fin with 22-24 rays (X= 22.6, mode= 22, cv= 3.3), its base 3.3-4.5 % SL, its length 16-21 % SL. Pelvic fin with two long rays; in one individual only, three small rays observed beneath skin. Caudal fin asymmetrical, upper procurrent rays 7-10 (X= 8.5, mode= 9, cv= 9.8), six principal rays, lower procurrent rays 11-13 (X= 12.3, mode= 12, cv= 4.8). Total vertebrae 51-54 (X= 52.6, mode= 53, cv= 1.7), precaudal vertebrae 15, caudal vertebrae 36-39 (X= 37.6, mode= 38, cv= 2.4). Gill rakers 4-6 (X= 5.1, mode= 5, cv= 7.8) + 11-14 (X= 12.5, mode= 12, cv= 7.1), total= 16 -19. Scales on a straight line 105-130, scales above lateral line 9-15 (X= 10.4, mode= 9, cv= 25.0), scales below 21.

Color in alcohol: Body gray, second dorsal fin dark brown to light gray to yellowish; visceral area always gray.

Distribution: This species is distributed along the Mid-Pacific Ridge, from the Kyushu-Palau Ridge (28° 05'N, 134° 42'E), off the south coast of Oahu Island, to Sala y Gomez Ridge in the eastern South Pacific. Okamura (1982) described it as _L. palauense_ from the Kyushu Palau Ridge, and Parin (1984) listed it from the Sala y Gomez Ridge. Collected at depth from 95-300 to 550 m (Fig. 23).

Comments: Even though the species is widely distributed, we found little evidence of differentiation. A principal component analysis of HL, PDL, PAL D2L and AL did not indicate geographic groupings (Fig. 37). Parin (1984), based on general appearance and meristic counts, considered _L. palauense_ a junior synonym of _L. rhodochir_. Our meristic data support Parin (Table 8).

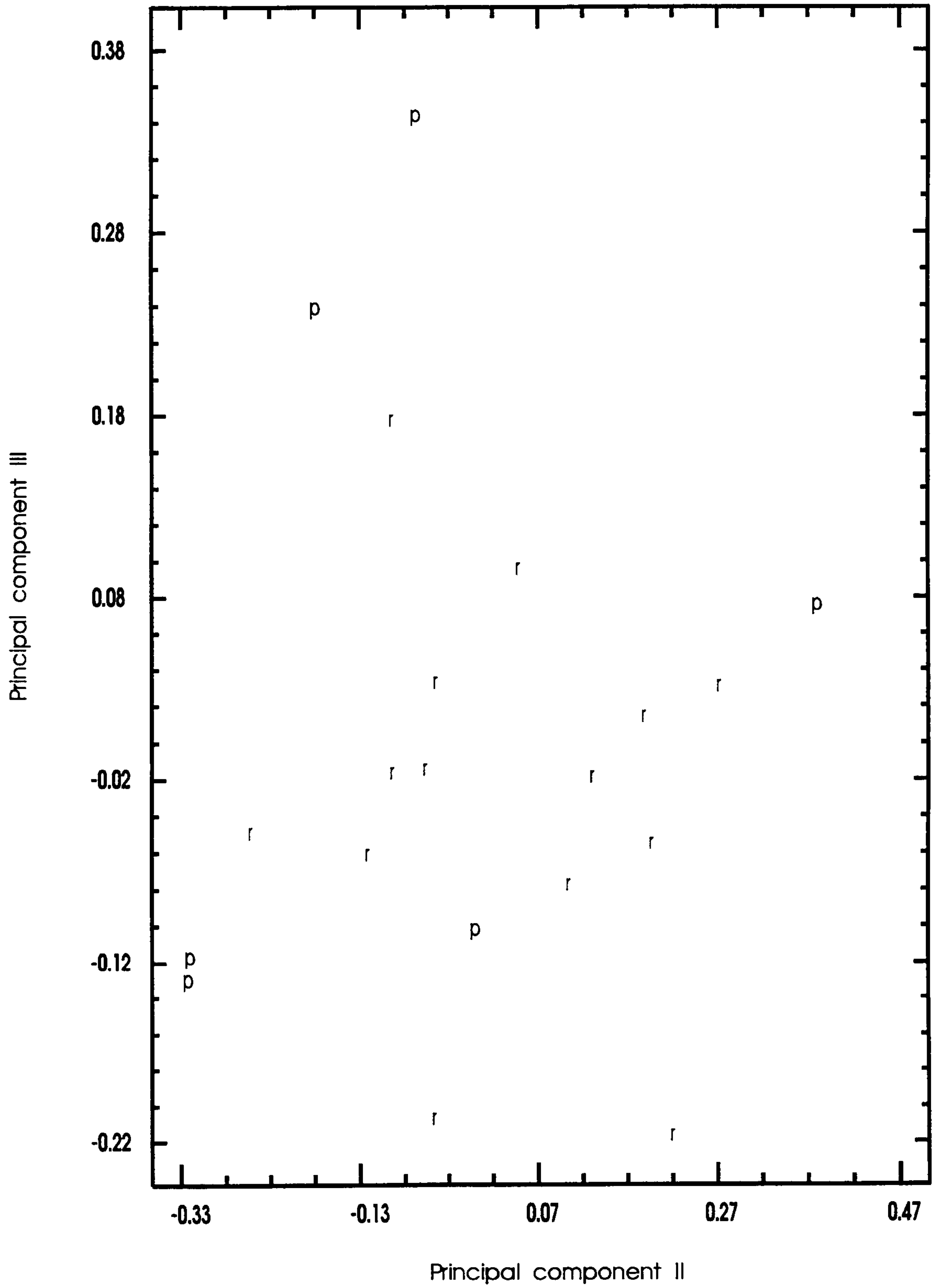


Fig. 37. Principal component analysis of morphometrics characters for L. rhodochir (r=Hawaii and Sala y Gomez Ridge, p=Kyushu Palau Ridge).

Table 8.- Comparison between selected meristic characters from adults of <u>Laemonema rhodochir</u> from Khyshiu Palau Ridge, Hawaii, Nazca and Sala y Gómez Ridge.

	D2						A						
	61	62	63	64	65	66	57	58	59	60	61	62	63
Khyshu Palau	1			3		1	1	1			2	1	
Hawaii		1						1					
Nazca & Sala y Gómez	1		1	4	4	3		2	1	2	4	3	1

	PCV	CV				TV				P1		
	15	36	37	38	39	51	52	53	54	22	23	24
Khyshu Palau	1		1				1			1	1	
Hawaii	1			1					1			1
Nazca & Sala y Gómez	13	2	3	6	2	1	3	6	1	7	5	2

	LGR				UGR			UPC				LPC		
	11	12	13	14	4	5	6	7	8	9	10	11	12	13
Khyshu Palau	1		3	1		1					1		1	
Hawaii				1		1			1					1
Nazca & Sala y Gómez	1	9	3	1	1	11	2	2	3	8		1	8	4

Laemonema rhodochir is similar to L. laureysi and L. n.sp. g as discussed above. Laemonema rhodochir differs from L. robustum in having more second dorsal fin rays (61-66 vs 50 -57), more anal fin rays (58-63 vs 48-54), fewer pectoral fin rays (22-24 vs 26-30), and fewer scales below the lateral line (21 vs 39-43). Laemonema rhodochir differs from L. yuvto in having more anal fin rays (58-63 vs 53), and fewer pectoral fin rays (22-24 vs 31). Laemonema rhodochir differs from L. n.sp. i, mainly in the length of the pelvic fin rays (19.8-35.2 vs 49-65 % SL).

Material examined: BSKU 35967 (1, 150 mm SL), paratype, 28° 05'N, 134° 42'E, 550 m, 17 I 1980. (paratype of Laemonema palauense). PPSIO uncat. (1, 198 mm SL), 24° 47'N, 135° 20'E, 340-360 m, 6 I 1982. PPSIO uncat. (3, 99-178 mm SL), 25°41'S, 86°35'W, st 1940, 28 IV 1987. PPSIO uncat. (3, 107-127 mm SL), 25°48'S, 86°34'W, 28 IV 1987. PPSIO uncat. (2, 200-208 mm SL), 25°42'S, 86°32'W, 420 m, 31 X 1979. PPSIO uncat. (1, 208 mm SL), 25°07'S, 99°46'W, 330-356 m, 7 V 1987. PPSIO uncat. (1, 88 mm SL), 25°09'S,90°18'W. USNM 51623 (1, 104 mm SL), Holotype, 02° N, 02° 24'E, 53-211 fm, 27 III 1902. USNM 265089 (1, 191 mm SL), 25° 42'S, 86° 32'W, 420 m

Laemonema robustum Johnson, 1862

(Fig. 38)

Laemonema robustum Johnson, 1862: 167-180.

Laemonema robustum: Günther, 1862:357-358. Johnson, 1863: 62-64 (description). Goode and Bean, 1896: 362. Holt and Byrne, 1908: 87. Matsubara, 1938: 62. Taki, 1953: 208. Rass, 1954: 8, Parin, 1984: 57. Cohen, 1986: 717. Edwards and Glass, 1987: 630-631. Biscoito and Maul, 1989: 2-3. Parin and Sazonov, 1990: 6-8. Cohen et al., 1990: 361.

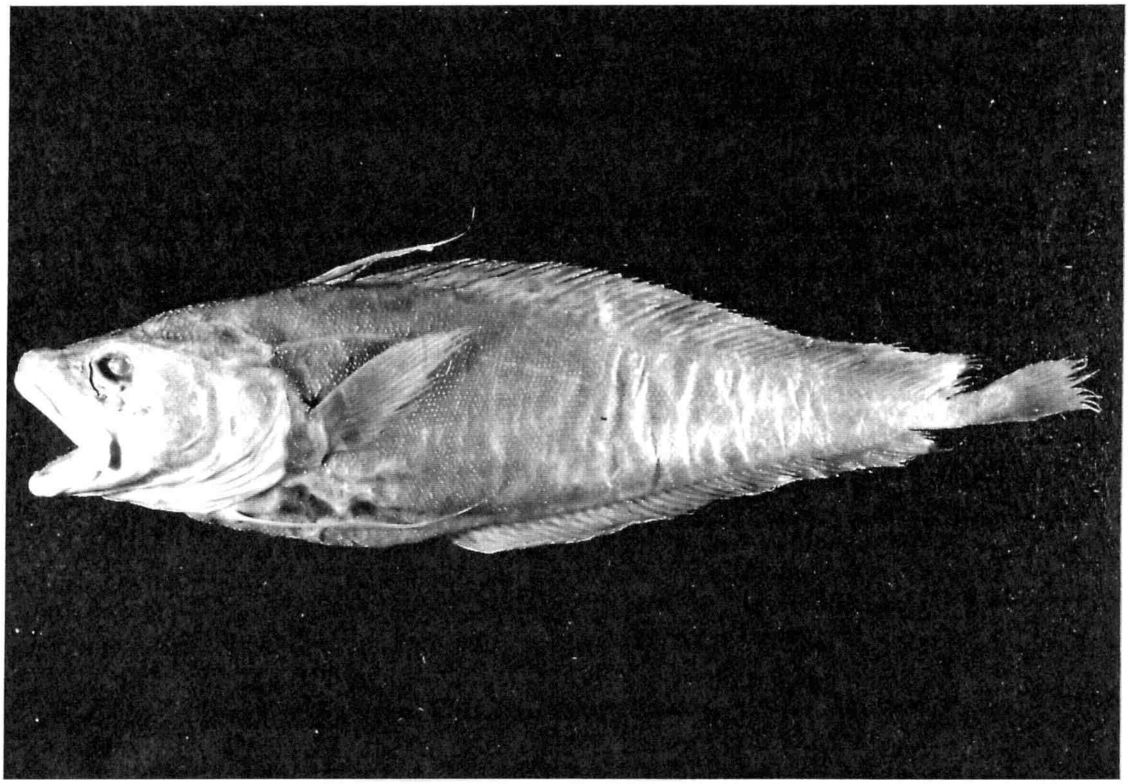


Fig. 38. Laemonema robustum Johnson, 1862
MMF 52 (271 mm SL)

Laemonema robustum (not of Johnson): Vaillant, 1888: 286.

Laemonema filodorsale Okamura,1982: 132-135 pp.

Laemonema filodorsale: Parin,1984:57. Okamura, 1984:92. Parin and Sazonov, 1990:6. Cohen et al., 1990:361.

Haloporphyreus modestum Franz, 1910:28-29.

Laemonema modestum (Franz): Nakaya et al, 1980:41. Okamura,1984: 92. Cohen et al.,1990:361.

Laemonema sp. : Fourmanoir and Rivaton, 1979:416, Parin, 1984:57.

Diagnosis: Body robust and deep 21.9-27.7 % SL, with deciduous scales; pectoral fin with 26-30 rays; scales below lateral line 39-47.

Description: Head length 24.9-29.9 % SL; mouth large, almost terminal. Maxillary 12.4-14.8 % SL, reaching end of orbit, with external row of strong caniniform teeth, followed by at least seven rows of smaller canine like teeth; a gap at symphysis. Vomer with caniniform teeth on a rounded patch. Dentary with outer row of strong caninelike teeth, followed by two or three rows of small teeth; a small gap at dentary symphysis. Snout without scales, short 6.9-8.4 SL %, with two nostril widely separated from eyes. Orbit diameter short, 5.3-7.3 % SL, wider than interorbital width, 4.7-6.1 % SL. Barbel 3.1-5.7 % SL. Postorbital length 12.1-16.3 % SL.

Predorsal fin length 27.2-32.6 % SL, about equal to prepectoral length 28.2-31.6 % SL. Prepelvic fin length 20.6-26.4, shorter than two previous measurements. Preanus length 38.9-45.0 % SL, less than preanal fin length, 41.9-50.0 % SL. Maximum depth of body 21.9-27.7 % SL; depth at anus 21.7-27.5 % SL, depth at first anal fin ray 21.0-27.6 % SL. Body declines in depth to caudal peduncle, 2.4-3.5 % SL, which is larger than barbel.

First dorsal fin with six rays, its base 3.5-5.1 % SL, second ray longest 15.4-25.9 % SL, reaching at least first 10 rays of second dorsal fin; first ray very short and not visible. Second dorsal fin with 50-57 rays (X= 54.2, mode= 55, cv= 3.6), its base 55.5-66.9 % SL, ray lengths decreases with decreasing body depth. Anal fin with 48-54 rays (X= 50.8, mode= 50, cv= 3.0), its base 45.4-52.7 % SL; ray lengths decrease with body depth. Pectoral fin with 26-30 rays (X= 27.8, mode= 28, cv= 4.1), its base 3.5-5.4 % SL, its length 17.9-21.7 % SL. Pelvic fin with two rays, reaching at least fourth anal ray, its length 19.8-35.2 % SL. Caudal fin asymmetrical, lower procurrent rays 12-17 (X= 15, mode= 15, cv= 9.4), principal rays 6, upper procurrent rays 10-12 (X= 10.8, mode= 11, cv= 6.2). Total vertebrae 47-52 (X= 50.0, mode= 51, cv= 2.8), precaudal vertebrae 13-15 (X= 13.6, mode= 13, cv= 4.9), caudal vertebrae 34-38 (X= 36.4, mode= 36, cv= 3.3). Gill rakers 4-7 (X= 4.9, mode= 5, cv= 16.7) + 13-16 (X= 14.0, mode= 13, cv= 6.8), total= 17-22. Scales on a straight line 120-150, scales above lateral line 14-19 (X= 17.6, mode= 19, cv= 10.5), scales below lateral line 39-47 (X= 41.5, mode= 43, cv= 6.0).

Color in alcohol: Body light brown; visceral area gray; first dorsal fin and anterior portion of second dorsal fin dark brown.

Distribution: This species is widely distributed in the Atlantic and Pacific. In the Atlantic, it is found from the eastern North Atlantic near Madeira, the type locality, to Saint Helena Island (15° 58'S, 5° 43'W) in the tropical South Atlantic. Most specimens from the Atlantic were collected in the fish market at Funchal, Madeira (MMF), with no depth of capture data available. In the Pacific, L. robustum is found from the Kyushu-Palau Ridge to New Caledonia and Australia at depths from 336 to 800-1200m (Fig. 31). The wide distribution is found in other morid, Antimora rostrata, which is distributed in all oceans except the North Pacific (Small, 1981).

Comments: Laemonema robustum is the type species for Laemonema, because Johnson in June 1862, describe it originally under Günther's Laemonema. It was also redescribed by Günther in Nov 8, 1862, in the work in which Günther erected Laemonema for Phycis yarrelli Lowe. The holotype was examined for this study but unfortunately was lost in the mail when returned to BM(NH).

We found no morphological or meristic characters (Table 9) to differentiate L. robustum from L. filodorsale, L. modestum, and specimens from off eastern Australia and New Caledonia. We tentatively treat L. filodorsale and L. modestum as junior synonyms of L. robustum, but note the

Table 9.- Comparison between selected meristic characters of <u>Laemonema</u> <u>robustum</u> from Atlantic Ocean and Western Pacific Ocean.

	D2								A						
	50	51	52	53	54	55	56	57	48	49	50	51	52	53	54
Atlantic Ocean	1		2	2	1		1		1	1	3	1		1	
Japan and Kyushu Palau Ridge			1		1	4	1	1		1	2	2	3		
Australia and New Caledonia						1		1					1		1

	PCVERT			CVERT					P1				
	13	14	15	34	35	36	37	38	26	27	28	29	30
Atlantic Ocean	5	1		1		2	2	1		2	2	3	
Japan and Kyushu Palau Ridge		3		1	1	1			1	1	4		1
Australia and New Caledonia		1	1			1		1	2				

	LOWGRAK				UPPGRAK			
	13	14	15	16	4	5	6	7
Atlantic Ocean	1	2	4		1	5		1
Japan and Kyushu Palau Ridge	5	3			4	4		
Australia and New Caledonia			1	1			2	

small sample sizes and the potential that slight differences might exist. Small (1981) reached similar geographic conclusions about the widely-ranging morid, Antimora rostrata, and found only slight differences in selected morphometric measurements.

Laemonema robustum is morphologically similar to L. n. sp. i, from the western Indian Ocean, and L. yuvto, from the eastern Southern Ocean, in the robustness of the body, the low fins ray and vertebral counts, and the high pectoral fin ray counts. Laemonema robustum differs from L. yuvto in having fewer second dorsal fin rays (50-57 vs 62). Differences from other species have been discussed above.

Material examined: BM(NH)1862.6.9 (1, 311 mm SL), tail regenerated, holotype. Madeira Island. BM(NH)1969.3.1 (1, 367 mm SL), St. Helena Island, Central South Atlantic. BSKU 29532 (1, 294 mm SL), paratype, 26° 45'N, 135° 19'E, 336 m, 17 XII 1979. CAS-SU 123939, (1, 270 mm SL), Totomi, Hondo, NW and Central Pacific, Japan, 1 February 1903. MMF 52 (1, 271 mm SL), Funchal fish market, 4 V 1940. MMF 3127 (1, 265 mm SL), Funchal fish market, 17 I 1950. MMF 3128 (1, 309 mm SL) (specimen cleared and stained), Funchal fish market, 3 II 1950. MMF 3461 (1, 306 mm SL), Funchal fish market, 17 V 1952. MMF 3512 (1, 312 mm SL), Funchal fish market, 30 VII 1952. MNHN 1986-295 (1, 203 mm SL), New Caledonia. MSU P 16049 (1, 281 mm SL), 27° 55'N, 134° 44'E, 800-1200 m. QM I.21006 (1, tail broken, 300 mm), 27° 46'S, 153° 58'E, 540 m.

Laemonema verecundum (Jordan and Cramer, 1897)

(Fig. 39)

Lepidion verecundum Jordan and Cramer in: Gilbert, 1897: 456-457.

Microlepidium verecundum (Jordan and Cramer in: Gilbert, 1897). Garman, 1899:180.

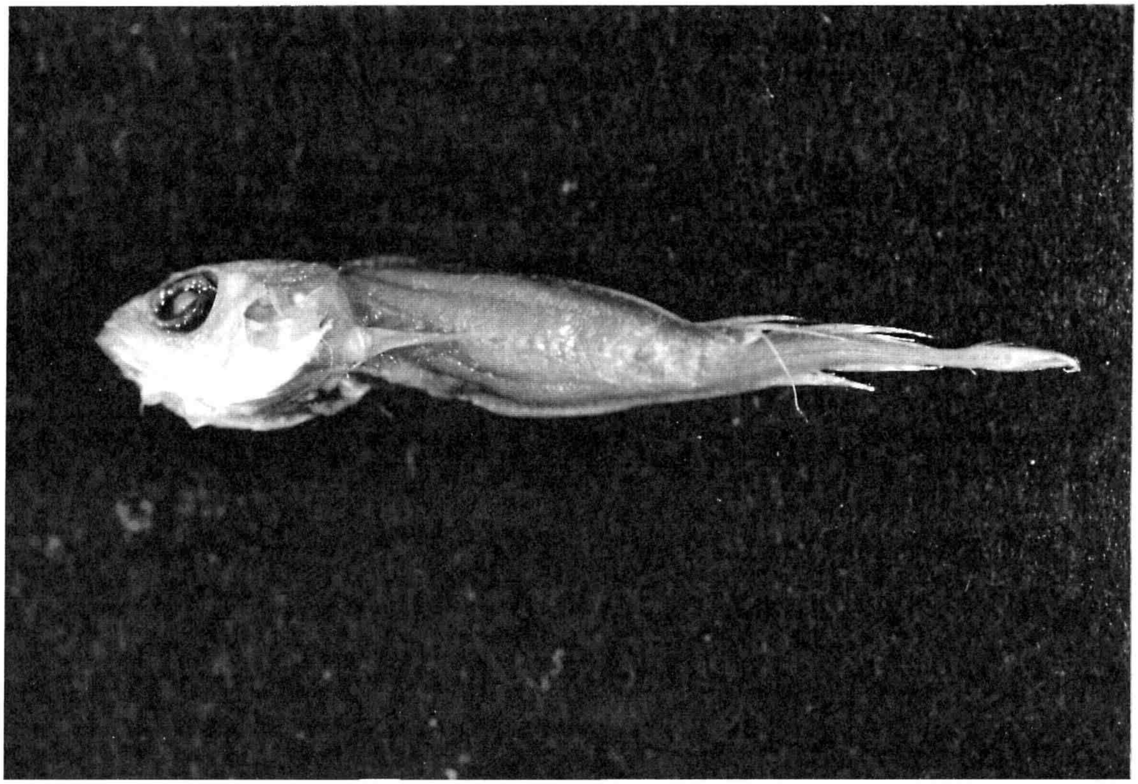


Fig. 39. Laemonema verecundum (Jordan and Cramer, 1897)
LACM 31118-2 (60 mm SL)

<u>Laemonema</u> <u>verecunda</u> (Jordan and Cramer <u>in</u>: Gilbert, 1897): Cohen et al., 1990:361.

Diagnosis: Body slender; vomer with a V-shape; first dorsal rays 8 to 9, second dorsal fin 40-42 rays, anal fin with 41 rays; barbel present, 1.2-1.7 % SL.

Description: Head 28.4-30.4 % SL, mouth subterminal, slightly inclined. Snout short, 4.9-5.3 % SL. Maxillary with external row of conspicuous canine-like teeth, and two inner rows of smaller canine-like teeth; a large space with no teeth at symphysis. Dentary with one row of conspicuous canine-like teeth, and one inner row of not well-defined small teeth; no symphyseal teeth gap. Teeth on vomer canine-like, in single V-shaped line. Small barbel on chin, 1.2-1.7 % SL. Orbit diameter, 9.1-11.2 % SL. Interorbital width short 3.6-4.7 % SL. Maxillary 12.1-12.6 % SL, ending at about same vertical as anterior part of pupil. Opercle ending in a spine in its upper portion. Postorbital length 15.1-15.6 % SL.

Greatest depth of body around anus area, 16.5 % SL. Body depth at first anal ray 14.8-17.5 % SL. Predorsal length 26.4-28.7 % SL. Preanal length 41.5-42.7 % SL; preanus length 39.8-40.9 % SL. Depth at anus 15.1-17.1 % SL. Caudal peduncle depth 1.7 % SL.

First dorsal fin with 8-9 rays, its base 7.9-8.4 % SL; first ray very short and not embedded in skin; third ray largest, 18.7 % SL. Second dorsal fin with 40-42 rays, base long, 51.0-53.6 % SL. Anal fin with 41 rays, base slightly shorter than second dorsal fin base, 49.0-50.4 % SL. Pectoral fin with 18-19 rays, its base 3.6-3.9 % SL, prepectoral length 27.1-28.9 % SL. Pelvic fin rays with two large fin rays which reach the first two anal rays, its length 28.1-30.0 % SL, evidence of at least two other short rays. Caudal fin asymmetrical, 11 upper procurrent rays, 6 principal rays, and 13 lower procurrent rays. Total vertebrae 42-43, precaudal vertebrae 12-13, caudal vertebrae 29-31. Gill rakers 5-6 + 12-14, total= 17-19.

Color in alcohol: Body light brown; head with branchial area yellowish; visceral area dark brown; all fins whitish.

Distribution: *Laemonema verecundum* is only known from the Pacific off Mexico. The holotype was captured near Clarion Island of the Revilla-Giggedo group, in 655 m. The other two individuals studied were captured in the Middle American Trench, 42 nautical miles from Cabo Corrientes Lighthouse, Mexico (Fig. 23).

Comments: Jordan and Cramer (in Gilbert, 1897) described this species under the genus *Lepidion*, even though they indicated that "...ventral apparently 4 (some rays broken on each side)." Later, Garman (1899), erected *Microlepidium* which differs from *Lepidion* in the following: "...longer first dorsal of eight rays instead of four, in having ventrals of four rays instead of six." Garman (1899) included *L. verecundum* under the genus *Microlepidium*. Cohen et al. (1990) include this species under the genus *Laemonema* but give no reasons, even though they stated that some of the species listed will be placed in other genera. Paulin (1989) indicated that Microlepidium and Podonematichthys may be synonyms, but he did not examine specimens of the former. This species resembles L. longipes and G. nana in having few total vertebrae, few second dorsal rays, and few anal fin rays. It differs from both species in having more first dorsal fin rays 8-9 rays (6 in L. longipes and 4-6 in G. nana). The high number of dorsal fin rays, the low number of caudal vertebrae, and the low counts in the second dorsal and anal fins distinguish L. verecundum of all other species of Laemonema.

Material examined: LACM 31118-2 (2, 60 - 77.5 mm SL), Mexico: Middle American Trench, 42 miles from Cabo Corrientes Lighthouse, 19 I 1970 (one specimen cleared and stained). USNM 47748 (1, 52 mm SL), Holotype, near Clarion Is. 15° 32'N, 124° 19'W, 8 IX 1889.

Laemonema yarrelli (Lowe, 1841)

(Fig. 40)

Phycis yarrelli Lowe, 1841: 190.

Laemonema yarrelli: Günther, 1862: 356. Goode and Bean, 1896, 2:362. Holt and Byrne, 1908:87. Taki, 1953: 208. Rass, 1954: 8. Matsubara, 1938: 62. Parin, 1984:57. Cohen, 1986:717. Edwards and Glass, 1987:630. Biscoito and Maul, 1989:2-6. Cohen, 1990: 552. Cohen et al., 1990: 361.

Laemonema curtipes Biscoito and Maul, 1989:1-8.

Laemonema curtipes: Cohen et al., 1990:361.

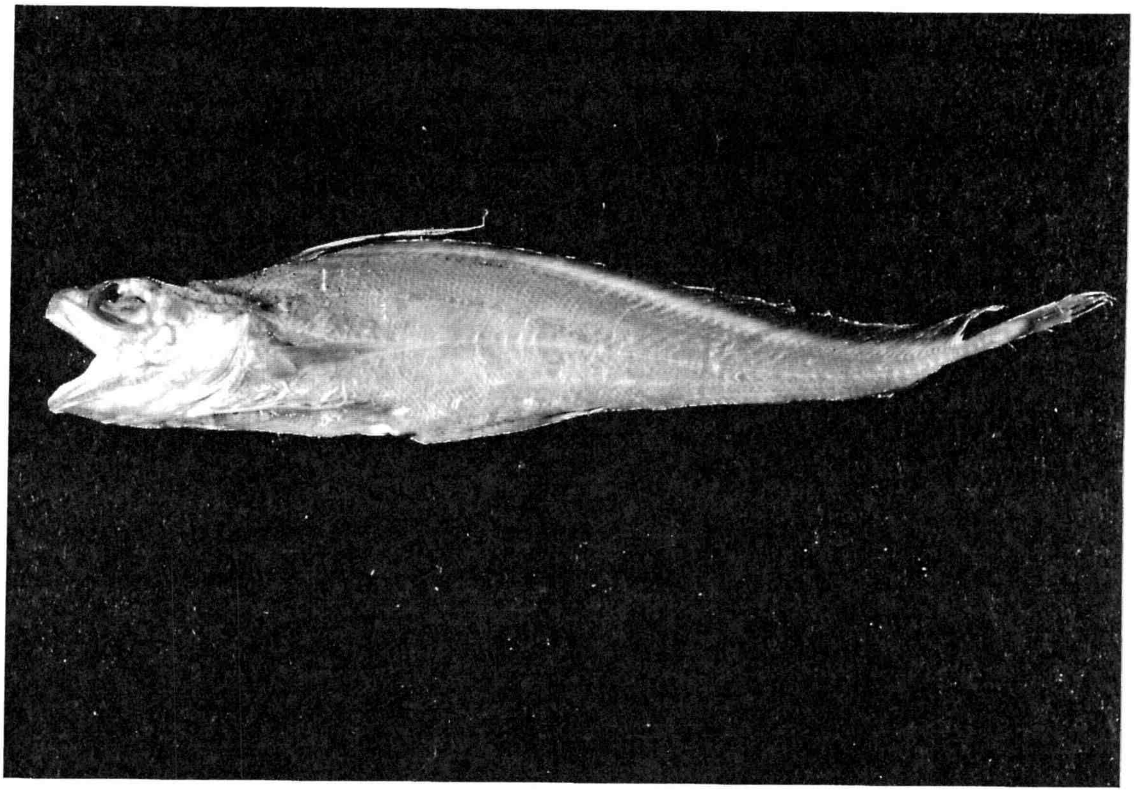


Fig. 40. Laemonema yarrelli (Lowe, 1841)
PPSIO uncataloged (155 mm SL)

Diagnosis: Body low and slender, covered with small, deciduous scales; second ray of first dorsal fin long, 18.5-27 % SL; vertical fins with an upper black stripe.

Description: Head short, 20.2-23.6 % SL. Mouth large, maxillary 9.5-10.9 % SL, with at least six or more rows of teeth that decrease in size from outer row to inside row. Teeth on small oval patch on vomer. Dentary similar to maxillary but with fewer rows of teeth. Barbel present 3.2-5.4 % SL. Snout 5.6-6.9 % SL, without scales. Eyes large, orbit diameter 6.3-7.6 % SL, greater than interorbital width, 3.7-5.0 % SL. Postorbital length 6.9-21.2 % SL.

Predorsal length 21.8-27.9 % SL, greater than head length. Maximum body depth 16.8-21.2 % SL, similar to depth at anus, 16.6-20.9 % SL. Prepectoral length 22.3-26.2 % SL, about same as predorsal fin length. Prepelvic length 14.8-22.6 % SL. Preanus length 32.2-40.3 % SL, slightly less than preanal fin length 35.3-43.5 % SL. Body decreasing in depth to caudal peduncle, which depth 1.8-2.5 % SL.

First dorsal fin with six rays, its base 3.6-5.7 % SL, second ray longest, 18.5-27 % SL, very strong; first ray beneath the skin. Second dorsal fin with 58-62 rays (X= 59.6, mode= 59, cv= 1.8), its base 64.6-71 % SL, rays gradually decrease towards end of fin. Anal fin with 57-62 rays (X= 59.1, mode= 58, cv= 2.2), its base 54.7-61.4 % SL, rays decrease moderately to middle of fin, then increases again. Pectoral fin with 21-25 rays (X= 22.9, mode= 22, cv= 5.0), its base 3.5-4.8 % SL, its length 15.6-19.5 % SL.

Pelvic fin rays with two long rays, its length 10.8-26.2 % SL; rays do or do not reach anus. Caudal fin asymmetrical, upper procurrent rays 6-7 (X= 6.8, mode= 7, cv= 6.1), principal rays 6, lower procurrent rays 11-12 (X= 11.5, mode= 11, cv= 4.5). Total vertebrae 52-54 (X= 53.1, mode= 53, cv= 1.1), precaudal vertebrae 15-16 (X= 15.8, mode= 16, cv= 2.1), caudal vertebrae 36-38 (X= 37.3, mode= 37, cv= 1.8). Gill rakers 6-8 (X= 6.3, mode= 6, cv= 9.5) + 14-18 (X= 16.3, mode= 16, cv= 5.3), total= 20-25. Scales on a straight line 100-111, scales above lateral line 8-9 (X= 8.4, mode= 8, cv= 6.2), scales below lateral line 18-23 (X= 21.6, mode= 23, cv= 9.5).

Distribution: Laemonema yarrelli is restricted to the eastern subtropical Atlantic and appears to be associated with seamounts and islands. Considered as benthopelagic on the outer shelf and upper slope by Cohen (1990). Lowe (1841) originally described it from Madeira. The others specimens studied were captured from The Meteor Seamount (29° 57'N, 28° 15'W), from the Seine Seamount (33° 45'N, 14° 20'W) at 220 m, and from 30° 04'N, 28° 18'W, at depth from 490-550 m (Fig. 23).

Color in alcohol: Body light brown, with some areas yellowish, probably because some specimens have lost portions of the skin. Recently collected specimens from Russian vessels have a light-brown body. Color of first dorsal fin most conspicuous, with a black membrane. Second dorsal and anal fins have black tips.

Comments: This species has been considered rare. The original description by Lowe (1841) was poor but improved by Günther (1862). Günther stated that the pectoral fin is rather longer than the pelvic fin, its length being equal to the distance of the anterior margin of the orbit from the extremity of the operculum. The specimens we examined had pectoral fin lengths of 15.6-19.5 % SL and pelvic fin lengths of 18.2-26.2 % SL. Thus, the pelvic fin is longer than pectoral fin. Pelvic fin length and barbel length were used by Biscoito and Maul (1989) to describe L. curtipes. Barbel length has a positive allometric relationship with size (Fig. 41, r= 0.77), and all meristic characters of L. curtipes are within the range of L. yarrelli. Laemonema yarrelli is similar to L. barbatulum in having a long first dorsal fin ray in adults (19.0-27.0 % SL and 12.2-31.9 % SL, respectively) and in adult coloration of the dorsal and anal fins. Differences with other species of Laemonema were discussed above.

Material examined: MMF 13874 (1, 128 mm SL), Funchal fish market, 5 V 1988. MMF 22386 (1, 156.5 mm SL), Meteor Seamount, 18 VII 1967. MMF 22543 (1, 140.7 mm SL), (same data MMF 2386). MMF 23858 (1, 186 mm SL), Holotype, Seine Seamount, 29 IV 1985, 220 m.(holotype of Laemonema curtipes). MSU P16047 (6, 147-206 mm SL), 29°57'N, 28°15'W, Great Meteor Seamount, 480 m, 28 VI 1982 (one specimen cleared and stained). PPSIO uncat. (2, 154-155 mm SL), 30°04'N, 28°19'W, 490-550 m. 26 VI 1982. USNM 304472 (5, 75.4-162 mm Sl), 17°23'S, 11°20'E, 366 m, 24 III 1968.

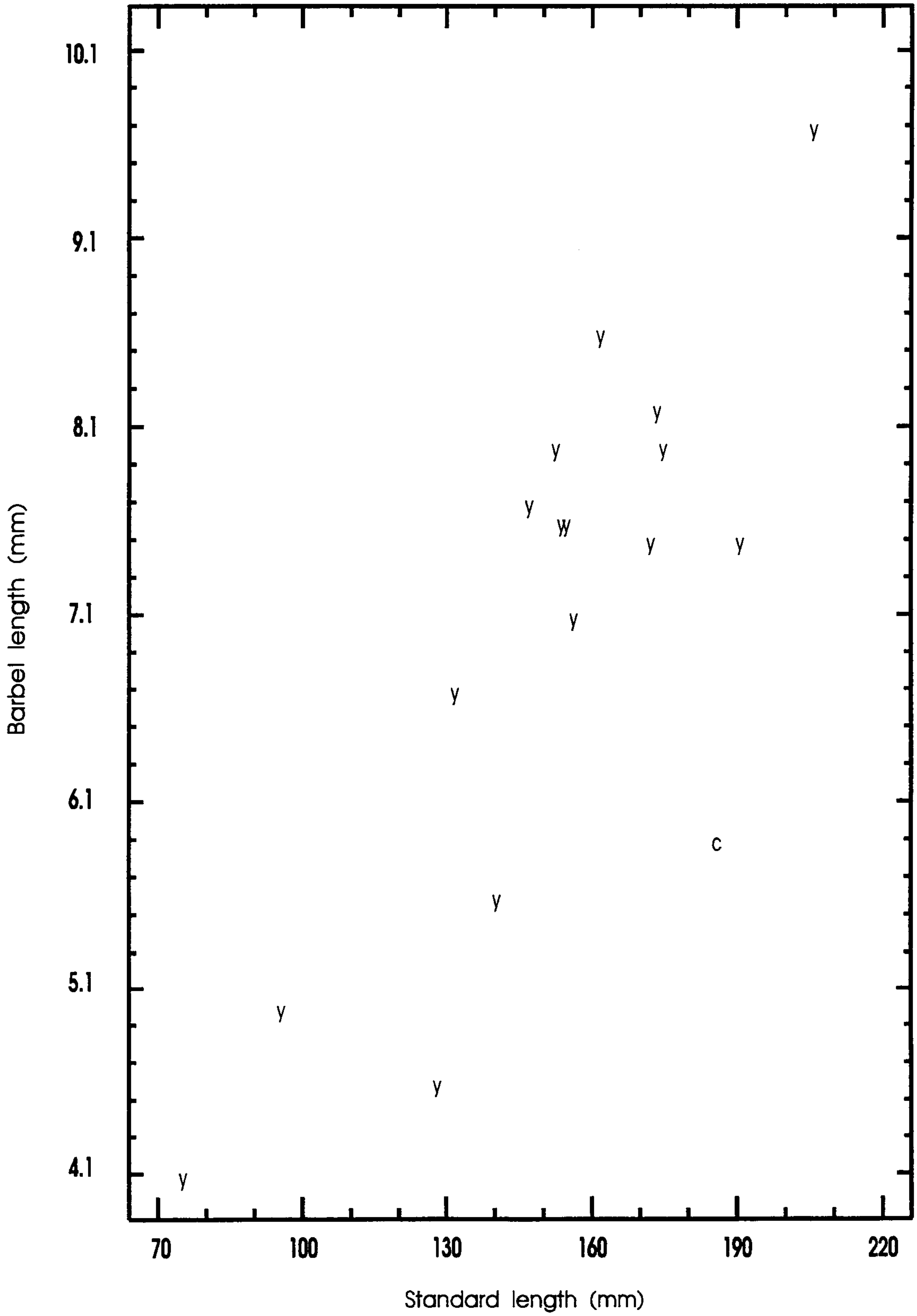


Fig. 41. Barbel length vs Standard length for L. yarrelli (y= L. yarrelli, c= Holotype of L. curtipes)

Laemonema yuvto Parin and Sazonov, 1990

Description: (from the original paper) No globular head; almost terminal mouth; maxillary extending to a vertical from posterior margin of pupil; both jaws without enlarged teeth, all teeth uniform; oral cavity unpigmented; well developed barbel; snout naked except for a band of embedded scales extending on each side from interorbital to level of anterior nostril. Interorbital space almost flat, equal to orbit diameter. D1 6, D2 62, A 53, P1 31, P2 2. Vertebrae 15 + 36 = 51. Modified lateral line scales 29-30, scales on a longitudinal row about 135, scales above lateral line 13. Gill rakers 13 + 5.

Holotype: ZIL 49186, mature female, 191 mm SL, Sala y Gomez Ridge, 25°10'S, 90°19'W, 1-2 May 1987, bottom shrimp trawl at 545-600 m (Fig. 31).

Remarks: According to Parin and Sazonov (1990), L. yuvto is related to L. robustum and differs mainly in the number of dorsal fin rays (62 vs 50-57). It is also similar to L. n.sp. i, but differs in the length of the pelvic fin rays (26.9 vs 49.2-63.6 % SL). Laemonema yuvto is different from all other Laemonema species because of the presence of modified scales on the lateral line. The modified scales are tubular according to Sazonov (pers. comm., 1995).

No specimens were available to examine.

Guttigadus Taki, 1953

Laemonema (Guttigadus) Taki, 1953:201-210; type species, Laemonema (Guttigadus) nana Taki, 1953 by monotypy).

Momonatira Paulin, 1985: 357 (type species, Momonatira globosus Paulin, 1985).

Paralaemonema Trunov, 1990: 81-83 (type species by original designation, P. nudirostre Trunov, 1990).

Diagnosis: Head globular; interorbital length usually greater than orbit diameter; vomer absent, rounded or v-shaped; a small barbel usually present on chin; bases of dorsal and anal fin generally fleshy; highly modified scales in lateral line; pelvic fin with two large rays plus one to three smaller rays; caudal vertebrae 41-50; anus usually well separated from anal fin.

Comments: Taki (1953) described Guttigadus as a subgenus of Laemonema based on Laemonema nana; because of the Rules of Priority Guttigadus, is the senior name and it is erected as a valid name for the genus. Paulin (1985) described Momonatira based on numerous features of G. globosus, one of which, the fleshy bases of the dorsal and anal fins, is supported herein as a synapomorphy of most Guttigadus. Trunov (1990) described Paralaemonema to include P. nudirostre, P. nudicephalum, and P. squamirostre. The diagnostic characters were a deeper body and a "casing" of skin on the anterior part of the bases of the dorsal and anal fins, but Trunov acknowledged the presence of the latter in Guttigadus. Based on the analysis above, Paralaemonema and Momonatira are treated as a junior synonyms of Guttigadus, and G. nana, previously included in Laemonema, is included in Guttigadus.

Guttigadus globiceps (Gilchrist, 1906)

(Fig. 42)

Laemonema globiceps Gilchrist, 1906: 157-158.

Laemonema multiradiatum Thompson, 1916: 401-476.

Laemonema globiceps: Taki, 1953:8. Rass, 1954:5. Cohen, 1986. Paulin, 1983. Parin, 1984:57. Markle and Meléndez, 1989: 871, (redescription). Cohen et al., 1990:361 (list).

Laemonema multiradiatum: Rass, 1954:5.

Diagnosis: Body low and slender, covered by small, deciduous scales ending in a small, thin caudal peduncle; second ray of the dorsal fin long 25.5-50.7 % SL; gill rakers 10-13 + 22-30 = 33-43.

Description: Head 17.7-24.7 % SL; mouth almost terminal. Snout short, 6.4-7.8 % SL. Maxillary with villiform teeth and an external row of canine-like teeth, with three additional rows of relatively small villiform teeth. Dentary with two rows of small canine-like teeth, external ones slightly larger than internal ones. Teeth on vomer canine-like, on a small rounded patch. Barbel on chin very small, occasionally present, 0.4-0.5 % SL. Orbit diameter, 4.2-6.3 % SL, at least four times in head length. Interorbital wide, 7.5-11.4 % SL, more than twice in head length, almost twice in orbit diameter. Maxillary 10.6-13.5 % SL., ending at

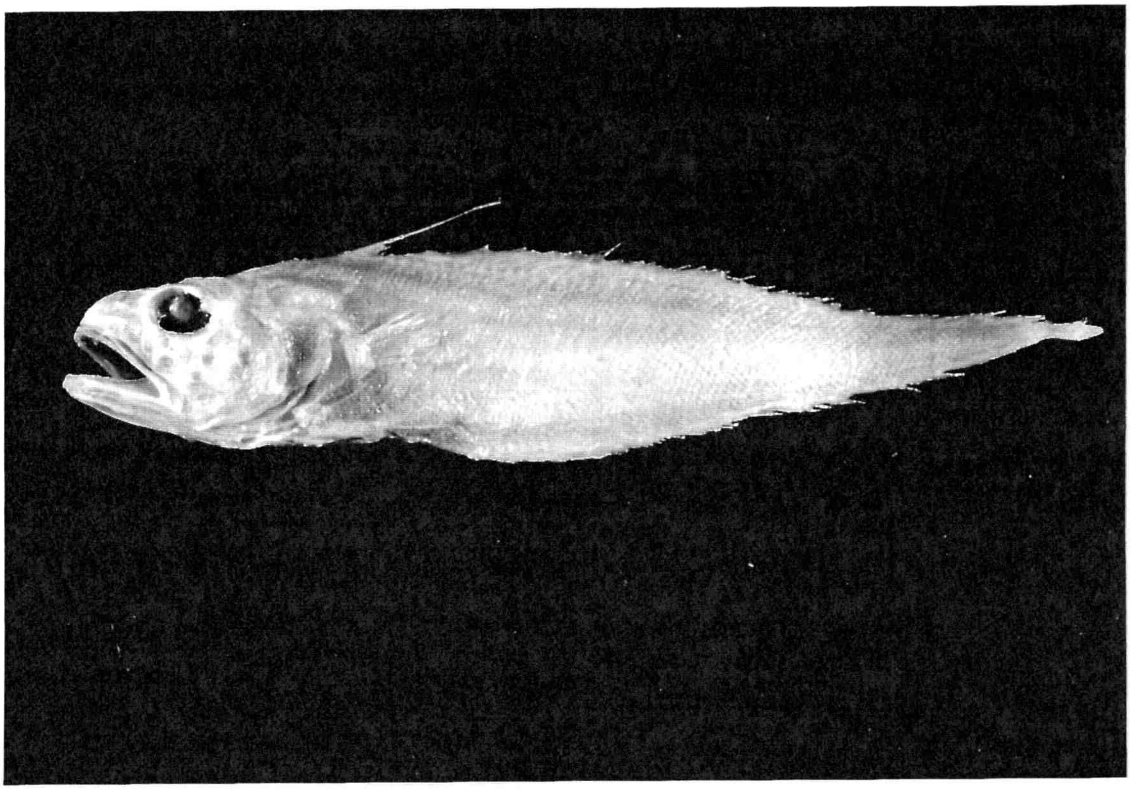


Fig. 42. Guttigadus globiceps (Gilchrist,1906)
MSU 15857 (158 mm SL)

about same vertical as posterior end of orbit. Opercle bone thin, not ending in a spine in its upper portion. Postorbital length 5.7-12.3 % SL.

Greatest body depth before area of anus, 13.1-21.7 % SL. Depth at first anal fin ray 12.4-19.6 % SL. Anus and anal fin separated by distance greater than height of caudal peduncle. Preanus length 25.0-32.2 % SL. Preanal fin length 31.1-39.9 % SL. Predorsal length 22.1-27.1 % SL. Depth at anus 12.0-19.6 % SL. Caudal peduncle depth 0.9-1.9 % SL.

First dorsal fin with 4-7 rays (X= 5.8, mode= 6, cv=10.6) base short, 3.2-4.5 % SL; first ray embedded in skin, second ray longest, 25.5-50.7 % SL, remaining rays gradually decrease in height. Second dorsal fin with 65-77 rays (X= 70.5, mode= 71, cv= 3.9), base long 65.9-74.0 % SL, rays gradually decrease in height posteriorly. Anal fin with 60-74 rays (X = 66.7, mode= 64, cv= 4.5), shorter than second dorsal fin 57.0-69.2 % SL. Pectoral fin with 18-21 rays (X= 19.5, mode = 19, cv= 13.3), its base 2.7-3.8 % SL, prepectoral length 22.9-26.9 % SL. Pelvic fin with two elongated rays and two or three smaller rays; length 9.4-27.5 % SL, reach extending pass vent to anal fin. Caudal fin asymmetrical, 9-12 lower procurrent rays (X= 10.3, mode= 10, cv= 6.8), upper procurrent rays 7-9 (X= 7.9, mode= 8, cv= 8.1), principal rays 5-6 (X= 5.96, mode= 6). Total vertebrae 55-62 (X= 58.9, mode= 58, cv= 2.8), precaudal vertebrae 11-13 (X= 11.95, mode= 12, cv= 4.0), caudal vertebrae 44-50 (X= 46.9, mode= 46, cv= 3.6). Gill rakers 10-13 + 22-30, total=

33-43. Lateral line not well defined, with modified scales <u>ca</u>. 20-24, on straight line about 85-105 scales. Scales above lateral line 7-8 (X= 7.6, mode= 8, cv= 7.0), below lateral line 15-25 (X= 19.1, mode= 18, cv= 18.5).

Color in alcohol: Body completely light brown to yellowish; all fins whitish; visceral area dark from black peritoneum; anterior area above head bluish, as are areas below orbit and operculum; mouth dark.

Distribution: <u>Guttigadus</u> <u>globiceps</u> is distributed widely in the Southern Ocean. It was described originally by Gilchrist (1906) from off Cape Point, South Africa. Thompson (1916) recorded specimens from off Lota, Chile, and described them as a new species (<u>Laemonema</u> <u>multiradiatum</u>). Paulin (1983) included <u>G</u>. <u>globiceps</u> in the New Zealand fauna. Markle and Meléndez (1989) redescribed the species from off Chile. It has been captured at depths between 730 and 1360 m (Fig. 43).

Comments: Gilchrist (1908) placed <u>G</u>. <u>globiceps</u> provisionally in <u>Laemonema</u>, explaining that the pelvic ray count of three rays did not agree with <u>Laemonema</u>. The species is characterized by its high number of gill rakers, both in the upper and lower arms (10-13 + 22-30), and the long second ray of the first dorsal fin (22.5-50.7 % SL). These two characters separate it from all other <u>Guttigadus</u>, which have a shorter second ray in the first dorsal fin and fewer gill rakers. <u>Guttigadus</u> <u>globiceps</u> also differs from <u>G</u>. <u>globosus</u> in having fewer pectoral fin rays (18 -21 vs 23-29) and

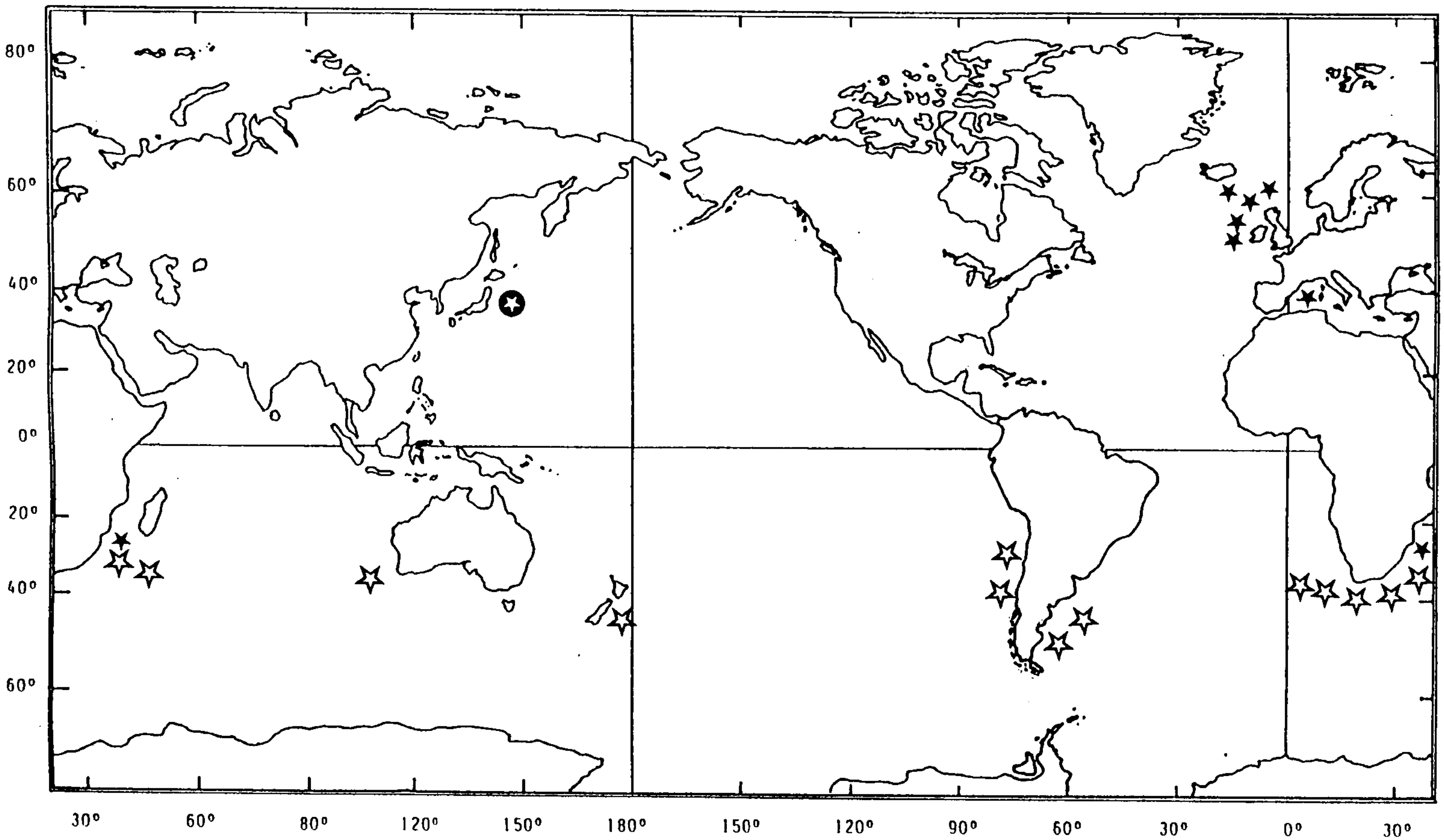


Fig. 43. Distribution map of <u>Guttigadus</u> <u>globiceps</u> (☆), <u>Guttigadus</u> <u>latifrons</u> (★) and <u>Guttigadus</u> <u>nana</u> (✪).

fewer upper and lower procurrent caudal fin rays (7-9 vs 10-12 and 9-12 vs 13-15, respectively). Guttigadus globiceps differs from G. kongi in having fewer pectoral fin rays (18-21 vs 22-27), more lower limb gill rakers (22-30 vs 13-21), and fewer lateral body scales (85-105 vs 170). Guttigadus globiceps differs from G. latifrons in having more upper and lower gill rakers (10 -13 vs 7-8 and 22-30 vs 14-17, respectively) and fewer scales on a straight line (85-105 vs 145-150). Guttigadus globiceps differs from G. nudicephalum in having more second dorsal fin rays (65-77 vs 59-62), fewer pectoral fin rays (18-21 vs 27-28), more caudal vertebrae (44-50 vs 36-38), and fewer scales above and below the lateral line (7 -8 vs 18-20 and 15-25 vs 40-55, respectively).

Material examined: AMS I.18712010 (5, 106-131 mm SL), 33° 49'S, 127° 09'E, 1100 m, 28 II 1976. ISH 187/67 (4, 143-153 mm SL), 33°47'S, 17°14'E, 1000 m, 25 VI 1967. LACM 44762-1 (1, 132 mm SL), off Western South Africa. MNHNC P6439 (1, 33.9 HL), 32° 53'S, 71° 47'W, 730 m, 2 IX 1980. MNHNC P6440 (3, 26.3-28.5 mm HL), 32° 06'S, 71° 46'W, 850 m, 14 I 1981. MNHNC P6566 (1, 31.4 mm HL), 34° 07'S, 72° 21'W, 850 m, 31 VIII 1980. MSU 16048 (2, 118 mm SL + tail broken), 25°24'S, 06°05'E, 900 m, 13 X 1979. MSU 17194 (1, tail broken), 31°10'S, 93°57'E, 1080 m 3 IV 1979. MSU 17201 (1, 136 mm SL), 31°30'S, 95°04'E, 1080-1150 m, 18 IX 1976. MSU 17206 (1, 141 mm SL), 33°32'S, 45°49'E, 1295 m, 25 VI 1976. MSU 15857 (1, 158 mm SL), 32°41'S, 01°48'E, 1060-1125 m, 3 IX 1979. MSU 17195 (1, 145 mm SL), 33°04'S,16°43'E, 1000 m, 24 I 1970. MSU P17200 (1, 142 mm SL), 32°30'S, 35°01'E, 1230-1270 m, 6 VIII 1976. MSU P17202 (2, 128 mm SL), 30°55'S, 93°28'E, 1150 m, 3 VIII 1977. MSU uncat. South Atlantic (cleared and stained). SAM 12445 (2, 93-143 mm SL), 36° 49'S, 21° 14'E, 500 fms. SAM 12447 (2, 143-145 mm SL), Cape Point E 3/4 N 38 miles, 630 fms. SAM 12448 (6, 149-162 mm SL), Cape Point E X N 3/4 N 34 miles, 480-600 fms. SAM 12450 (4, 142-155 mm SL), Cape Point N 64° E 64 miles. 700 fms. SAM 12488 (4, 117-143 mm SL), syntypes, Cape Point E 1/2 N 34 miles. 500 fms. SAM 12489 (1, 160 mm SL), Cape Point N E X E 1/4 E 38 miles. 755 fms. SAM 12490 (1, 148 mm SL), Cape

Point E 3/4 N 38 miles. 630 fms. SAM 12491 (1, 147 mm SL), Cape Point N 81° E 36 miles, 460 fms. SAM 12492 (3, 90-146 mm SL), Cape Point E 1/2 N, 36 miles, 700 fms. SAM 12493 (1, 160 mm SL), Cape Point N 81°E 32 miles, 460 fms. USNM 76858 (holotype of Laemonema multiradiatum). USNM 304551 (34, 99-153 mm SL), 33° 39'S, 72° 09'W, 1170 m, 10 VIII 1966. USNM 304558 (4, 109-134 mm SL), 34° 06'S, 72° 18'W, 5 VIII 1966. USNM 304557 (2, 101-153 mm SL), 32° 08'S, 71° 43'W, 960 m, 12 VIII 1966.

Guttigadus globosus (Paulin, 1985)

(Fig. 44)

Momonatira globosus Paulin, 1985: 357.

Momonatira globosus: Markle and Meléndez, 1989:875.

Trunov, 1989:179-185. Cohen et al., 1990:368.

Momonatira paulini Trunov, 1989:179-185.

Momonatira paulini: Cohen et al, 1990:368.

Diagnosis: Body deep; head large; caudal peduncle narrow; lower jaws included (overlapped by) upper jaws when mouth closed; interorbital very wide, 10.3-15.0 % SL; barbel on chin very short, 0.3-1.0 % SL; lining of mouth dark.

Description: Head length 22.4-28.6 % SL; scales lacking on head. Maxillary 8.8-12.5 % SL, its end reaching end of pupil; two or three rows of short caniniform teeth, plus one or two inner rows of small villiform teeth, that do not reach end of upper jaws. Dentary with one row of short, strong, caniniform teeth and a short row of inner teeth. Lower jaws included. Small, rounded vomer with teeth. Snout short, 6.7-10.0 % SL, larger than orbit diameter. Orbit diameter 4.5-7.5 % SL, smaller than interorbital width,

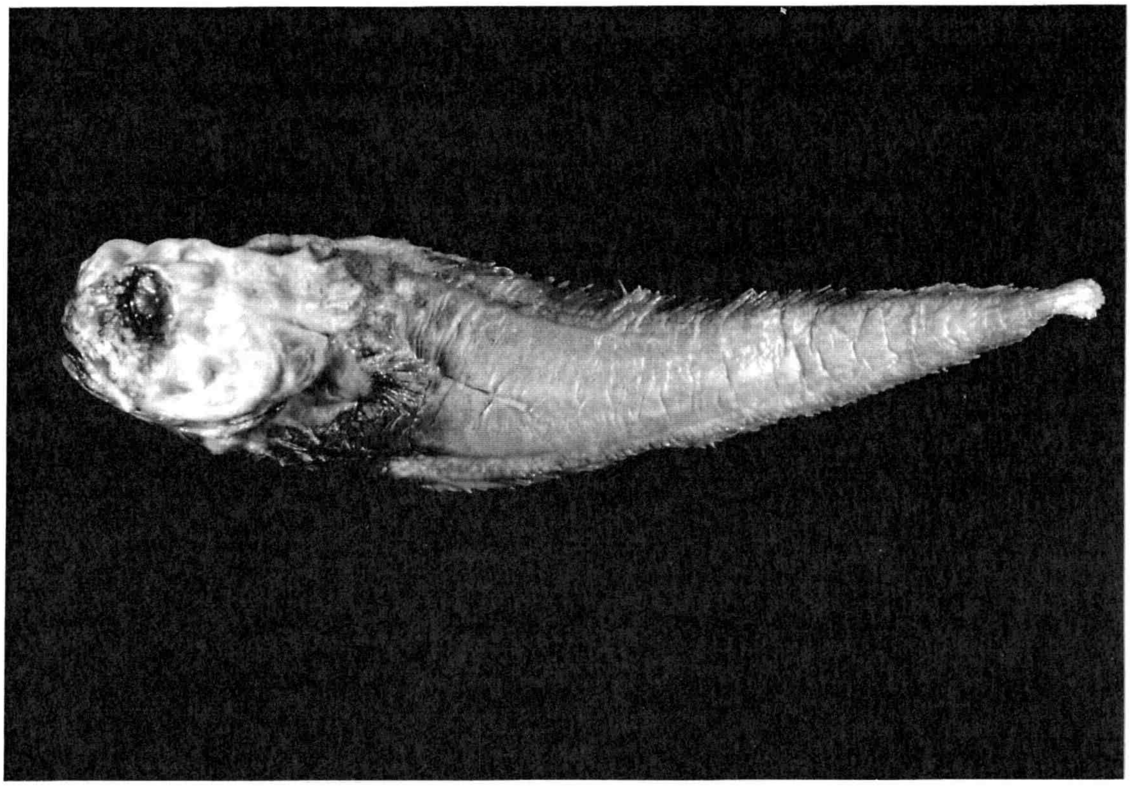


Fig. 44. Guttigadus globosus (Paulin, 1983) Paratype NMNZ 15861 (181 mm SL)

10.3-15.0 % SL. Barbel on chin very short 0.4-1.0 % SL. Postorbital length 11.0-14.4 % SL.

Predorsal length 25.3-34.8 % SL. Anus completely separated from anal fin, preanal length 30.6-42.6 % SL, preanus length 28.3-32.9 % SL. Pectoral fin inserted just before origin of first dorsal fin; prepectoral length 24.9-28.6 % SL. Pelvic fins well before insertion of pectoral and first dorsal fins; prepelvic length 17.5-22.3 % SL. Body at first anal ray 13.2-20.3 % SL.

First dorsal fin with 5-6 rays, very short, height 4.5-10.6 % SL. Second dorsal fin with 70-83 rays (X=77.3, mode= 78, cv= 4.6), its base 63.1-77.3 % SL; last rays of second dorsal and anal fin ending almost at same vertical. Anal fin with 73-84 rays (X= 76.7, mode=74, cv=6.0), its base 59.9-70.2 % SL. Pectoral fin with 23-29 rays (X=24.6, mode=25, cv=7.3), its base 3.8-5.1 % SL, its length 6.4-14.3 % SL. Pelvic fins with two long and three shorter rays, longest rays 4.0-13.9 % SL. Caudal fin asymmetrical, upper procurrent ray 10-12, principal rays 6, lower procurrent rays 13-14. Total vertebrae 56-59 (X=57.4, mode=57, cv=1.5), precaudal vertebrae 12-14 (X=12.8, mode=12, cv=7.1), caudal vertebrae 42-47 (X=44.5, mode 44, cv=3.5). Gill rakers 6-8 + 17-20, total= 23-28. Modified scales on lateral line ca. 16-25. Scales on a straight line 111 -137, scales above lateral line 12, scales below lateral line 27.

Color in alcohol: Body yellowish, visceral area dark brown. All fins have dark membranes. Head mostly whitish, except snout, below orbit, around mouth, and on dentary. Interior of mouth dark blue, gill chambers dark.

Distribution: Guttigadus globosus is known from New Zealand at depths of 1200-1500 m (Paulin 1985), and the mid South Atlantic (Trunov 1989, Cohen et al. 1990) (Fig. 45), at depths of 1175-1600 m.

Comments: Guttigadus paulini Trunov, 1989 is considered a synonym because of the overlap in all morphometric and meristic values. Some meristic counts suggest slight geographic or populational differences (Table 10), but we found no substantive diagnostic differences. The best diagnostic character, according to the literature, is the number of pyloric caeca: Paulin (1985) reports 3-4 for G. globosus and Trunov (1989) reports 10-11 for G. paulini. However, a paratype of G. globosus (NMNZ 15861) has 10 pyloric caeca, suggesting the need to re-evaluate Paulin's counts. In a related matter, Paulin (1985) reported high pectoral fin rays counts of 28-30 for G. globosus, but our counts in two paratypes (NMNZ 15828 and 15863) were 25 and 26, respectively.

Guttigadus globosus differs from G. kongi in having more total vertebrae (56-59 vs 49-56), fewer lateral body scales (111-137 vs 170), a longer anal fin base (59.9-70.2 vs 52.1-59.9), lower jaws included, and a pigmented rather than an unpigmented lining of the mouth. Guttigadus globosus appears to live deeper (1175-1600 m) than G. kongi (83-1400 m). Guttigadus globosus differs from G. latifrons in having

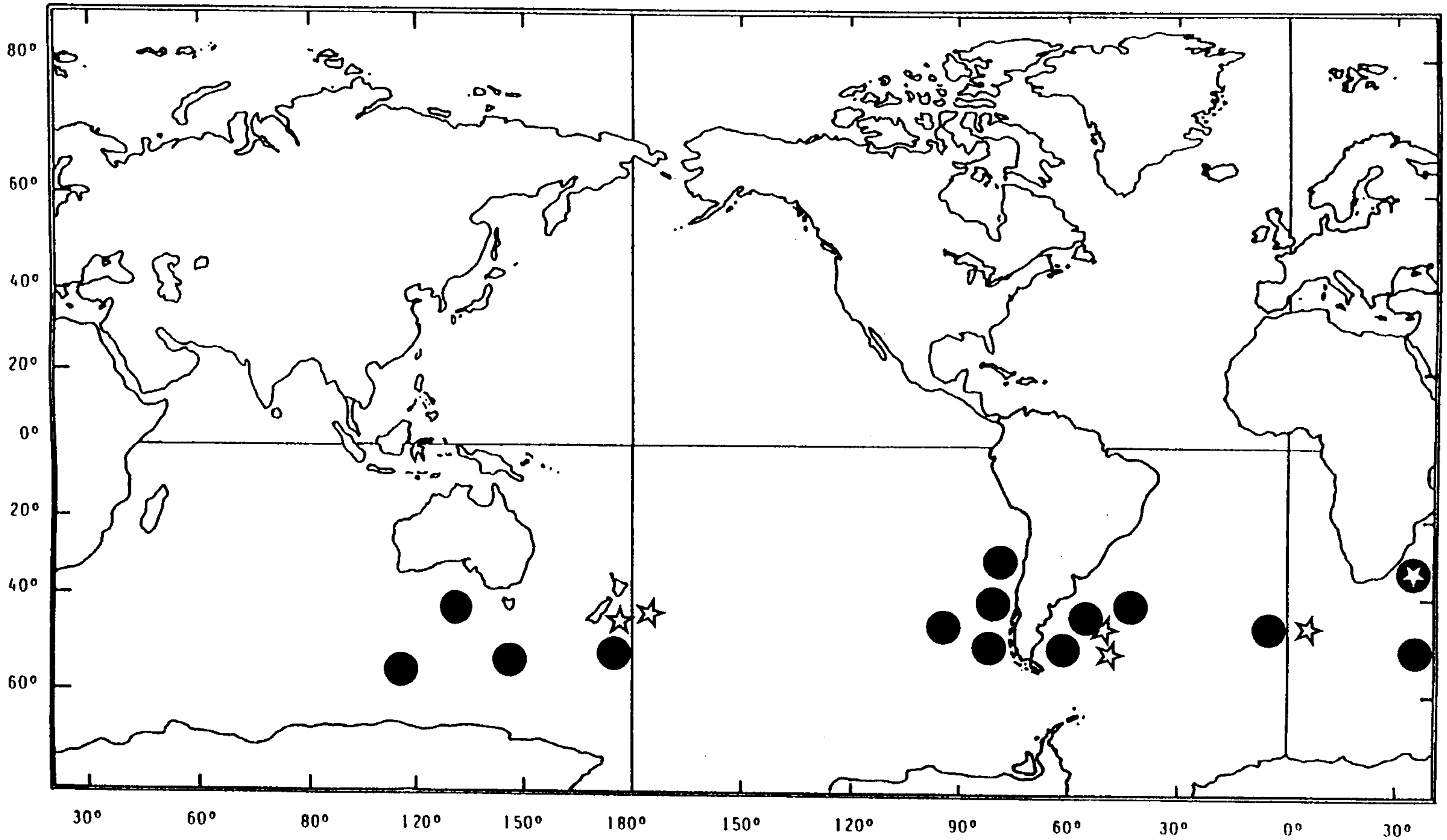


Fig. 45. Distribution map of Guttigadus globosus (☆), Guttigadus kongi (●), and Guttigadus nudicephalum (✪)

Table 10.- Comparison between selected meristic characters for <u>Guttigadus globosus</u> from New Zealand and South Atlantic Ocean.

	D2										A											
	70-74	75	76	77	78	79	80	81	82	83	70	-	73	74	-	76	77	-	81	82	-	84
New Zealand			1			1	1			1			1						1	1		1
South Atlantic	1	1		1	2						1			2		1	1					

	PCVERT			CV						TV			
	12	13	14	42	43	44	45	46	47	56	57	58	59
New Zealand	4	1	1			1	2	2	1		2	3	1
South Atlantic		2	3	1	1	2				1	3	1	

	LGR						UGR		
	17	18	19	20	21	22	6	7	8
New Zealand		1	1	2	1	1	1	2	1
South Atlantic	2	3					3	2	1

more lower limb gill rakers (17-20 vs 14-17), fewer scales below the lateral line (27 vs 38), a broader interorbital(10.4-14.8 vs 7.7-10.4 % SL), shorter barbel (0.3-1.0 vs 1.9-3.9 % SL), and inclusion of the lower jaws in the upper jaws. Guttigadus globosus differs from G. nudicephalum in having more second dorsal fin rays (70-83 vs 59-62), more anal fin rays (73-84 vs 56-60), more caudal vertebrae (42-47 vs 36-38), and more upper and lower gill rakers (6-8 vs 3-5 and 17-22 vs 10-11, respectively).

Material examined: NMNZ P15828 (1, 182 mm SL,paratype), 44°53'S, 172°48'E. 1180-1184 m. NMNZ P15861 (1, 181 mm SL, paratype), (same data as above). NMNZ P15863 (1, 133.6 mm SL), cleared and stained (same data as above). NMNZ P25203 (1, 194 mm SL), 46°54'-57'S, 174°26'-33'E, 1350 m. 23 XII 1989 (cleared and stained). MSU 16054 (1, 139 mm SL), 46°34'S, 59° 17'W, 1455-1560 m, 12 VIII 1974. MSU 16053 (2, 148-219 mm SL), 45°02'S, 59°32'W, 1240-1175 m, 10 VIII 1974. MSU 13720 (2, 129-139 mm SL), 42°53'S, 58°15'W, 1550-1600 m, 6 VIII 1974. MSU uncat. (1, 121 mm SL), 41°59'S, 00°25'E, 1250 m 12 XII 1979.

Guttigadus kongi (Markle and Meléndez, 1989)

(Fig. 46)

Laemonema kongi Markle and Meléndez, 1989: 871-876.

Laemonema kongi: Chiu et al., 1990. Cohen et al., 1990: 361.

Laemonema ? multiradiatum (not of Thompson,1916): Paulin, 1983:115. Pavlov and Andrianov, 1986:158.

Salilota sp.: Nakamura, 1986:106-107.

Diagnosis: Body short, broad, covered by small deciduous scales, ending in a very small caudal peduncle; 20-23 modified scales on lateral line; gill chamber, mouth floor

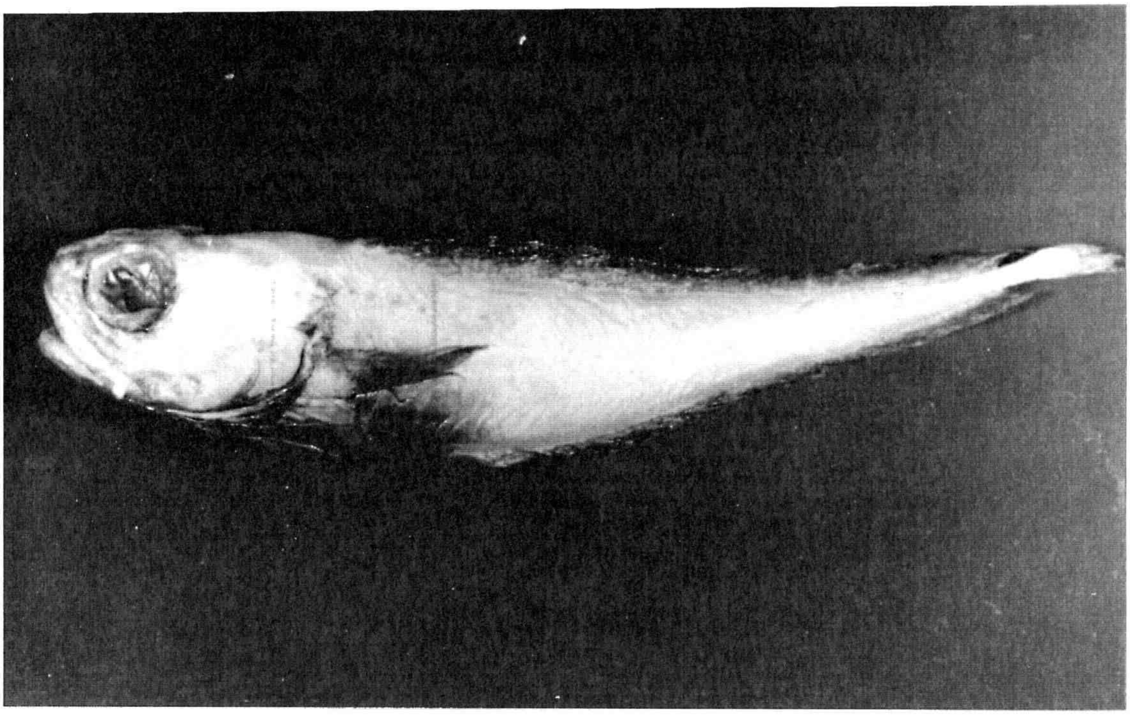


Fig. 46. Guttigadus kongi (Markle and Meléndez, 1989) Holotype MNHNC P 6438 (147 mm SL)

and lips without pigmentation; 49-56 total vertebrae; mouth subterminal.

Description: Head length 24.1-30.0 % SL; mouth subterminal slightly inclined; maxillary with one conspicuous row of strong caninelike teeth and shorter second row of much smaller caniniform teeth. Maxillary 12.2-15.1 % SL, ending almost at end of pupil. Dentary with conspicuous row of caniniform teeth. Vomer with rounded patch of caniniform teeth. Barbel on chin short, 0.7-3.8 % SL, sometimes absent. Orbit diameter short, 6.6-10.4 % SL, shorter than interorbital width, 7.0-13.1 % SL. Snout short, 6.6-12.9 % SL, about equal to orbit diameter. Postorbital length 11.4-14.9 % SL.

Predorsal fin length 26.2-32.9 % SL, slightly greater than head length. Preanal fin length 35.0-48.2 % SL. Preanus length 31.4-44.6 % SL. Maximum depth of body around area of anus, 20.1-31.0. Depth at first ray of anal fin 17.9-29.0 % SL, slightly less than maximum depth. Prepectoral fin length 26.8-33.0 % SL, shorter than predorsal length. Prepelvic fin length 20.1-31.1 % SL; pelvic insertion slightly anterior to pectoral fin. Body decreases in height continuously to caudal fin. Caudal peduncle depth 1.8-3.8 % SL, similar to length of barbel.

First dorsal fin with 4-7 rays (X= 5.4, mode= 6, cv= 15.0), second ray longest 5.5-12.1 % SL; base short 3.7-7.5 % SL; first ray not visible. Second dorsal fin with 62-78 rays (X= 69, mode= 71, cv= 4.6), its base 54.6-67.6 % SL;

rays gradually decrease in height to end of body. Anal fin with 61-75 rays (X= 65.7, mode= 64, cv= 4.9), its base 52.1-59.9 % SL; a shallow depression around middle of fin. Pectoral fin with 22-27 rays (X= 24.0, mode= 24, cv= 5.1), its base short 3.7-7.5 % SL, its length 13.2-21.6 % SL. Pelvic fin with 2 large rays and 1-4 smaller rays (X= 2.6, mode= 3, cv= 26.1); longest rays reach at least 10th anal ray; length 12.7-24.7 % SL. Caudal fin asymmetrical, upper procurrent rays 8-12 (X= 10.1, mode= 11, cv= 9.8), principal rays 5-6 (X= 5.9, mode= 6, cv= 5.0), lower procurrent rays 10-14 (X= 12.2, mode= 12, cv= 7.1). Total vertebrae 49-56 (X= 52.1, mode= 51, cv= 3.2), precaudal vertebrae 10-13 (X= 11.7, mode=12, cv= 6.1), caudal vertebrae 37-44 (X= 40.4, mode= 39, cv= 4.5). Gill rakers 6-10 + 13-21, total= 20-31. Lateral line with 20 to 23 modified scales, approximately 170 lateral body scales, 12 scales above, 35 scales below lateral line.

Color in alcohol: Body mainly pinkish (without scales); fins with dark membranes. Lips, interior of mouth, and gill chambers whitish or lightly pigmented. Juveniles with seven or eight thin, bluish vertical bands, lost at smaller sizes than in G. latifrons (which retains bars at sizes to 182 mm SL). Verticals bars present at 57 mm SL (NMNZ P 23396), but not in larger specimens (NMNZ P 9545, 68 mm SL, NMNZ 14852, 73 mm SL, and RUSI 27490, 86.7 mm SL).

Distribution: Mostly Southern Oceans; off Chile, Argentina, Southern Australia and New Zealand, at depths of 83-1500 m

(Fig. 45). Markle and Melendez (1989) indicated that G. kongi its more abundant at 500-800m. Our new data show an increment in the depth range given by the above authors from 1070 to 1500m, but maintain the more abundant depth range. Comments: Two lots referred to Laemonema "sp.?" by Markle and Meléndez (1989) may be tentatively identified. The western South Pacific specimen (NMNZ P9545, 68 mm SL) appears to be a juvenile G. kongi based on its total vertebral count of 53, which is in the range given for G. kongi. The two New South Wales, Australia, specimens (AMS E3210, 129 mm SL and damaged), with 59 total vertebrae remain problematic.

Guttigadus kongi is very similar to G. globosus (see above) and G. latifrons. Markle and Meléndez (1989) differentiated G. kongi from G. latifrons by its unpigmented mouth, lips, and gill chambers, and by its lower number of caudal vertebra. One Indian Ocean specimen of G. latifrons (PPSIO uncat. 101.5 mm SL) had an unpigmented mouth. The new data also show more overlap in caudal vertebrae (37-44 in G. kongi and 41-49 in G. latifrons) (Table 11), but modal differences remain strong. In addition, a PCA of the morphometric characters HL, PDL, PAL, PANUS, SNT, UJL, BARBEL, ORB, INT, D2L, AL, BD-IA, and CAUDDEPTH, indicated two groups representing G. kongi and G. latifrons, with some overlap (Fig. 47). When characters with the most variation (barbel length and caudal peduncle depth) are removed, the PCA also separated two groups, with some overlap (Fig. 48).

Table 11.- Comparison between selected meristic characters of <u>Guttigadus</u> <u>kongi</u> and <u>Guttigadus</u> <u>latifrons</u>.

	D1				D2																
	4	5	6	7	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
G. kongi	5	16	19	3	1		1	2	3	4	6	2	5	7	2	1	1	1			1
G. latifrons		13	13				2	1	1	3	3	1	1		4	2	2	2	2		

	A																PCV			
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	10	11	12	13
G. kongi	1	3	5	9	5	4	2	4		2	2			1	1		1	17	19	5
G. latifrons	1		1	2		3	3		3	2		2	3	2		1	1	7	13	6

	CV												
	37	38	39	40	41	42	43	44	45	46	47	48	49
G. kongi	1	5	10	8	3	7	5	1					
G. latifrons					1	1		3	3	6	7	4	4

	TV													P1						
	49	50	51	52	53	54	55	56	57	58	59	60	61	21	22	23	24	25	26	27
G. kongi	1	5	11	7	7	6		2							6	9	19	9	6	1
G. latifrons						1	1	4	3	7	5	3	2	8	7	8			1	

	LGR									UGR				
	13	14	15	16	17	18	19	20	21	6	7	8	9	10
G. kongi	3	4	12	8	8	9	1	2	2	8	17	6	14	4
G. latifrons		1	7	9	5						16	6		

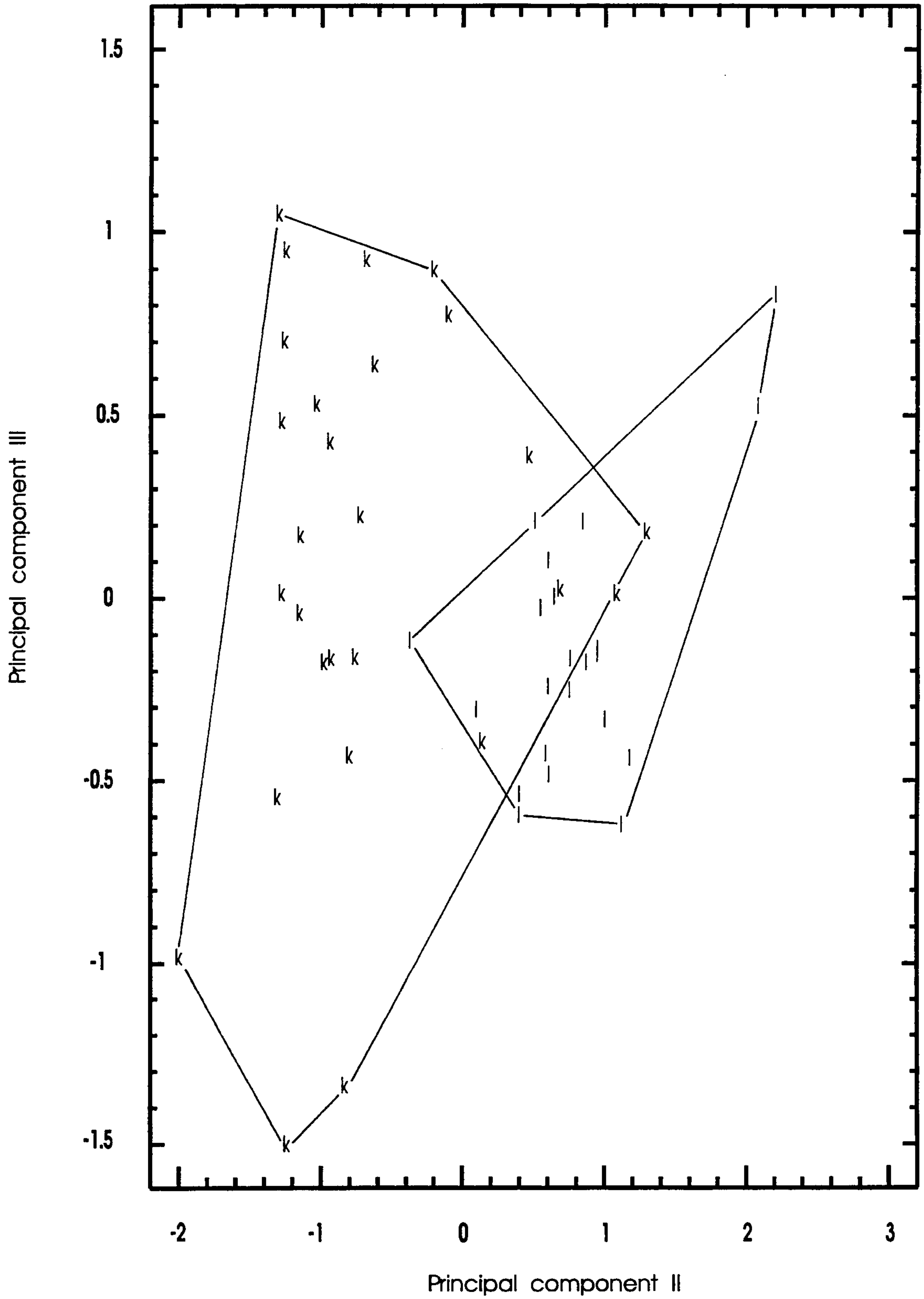


Fig. 47. Principal component analysis for morphometric characters for G. kongi (k) and G. latifrons (g).

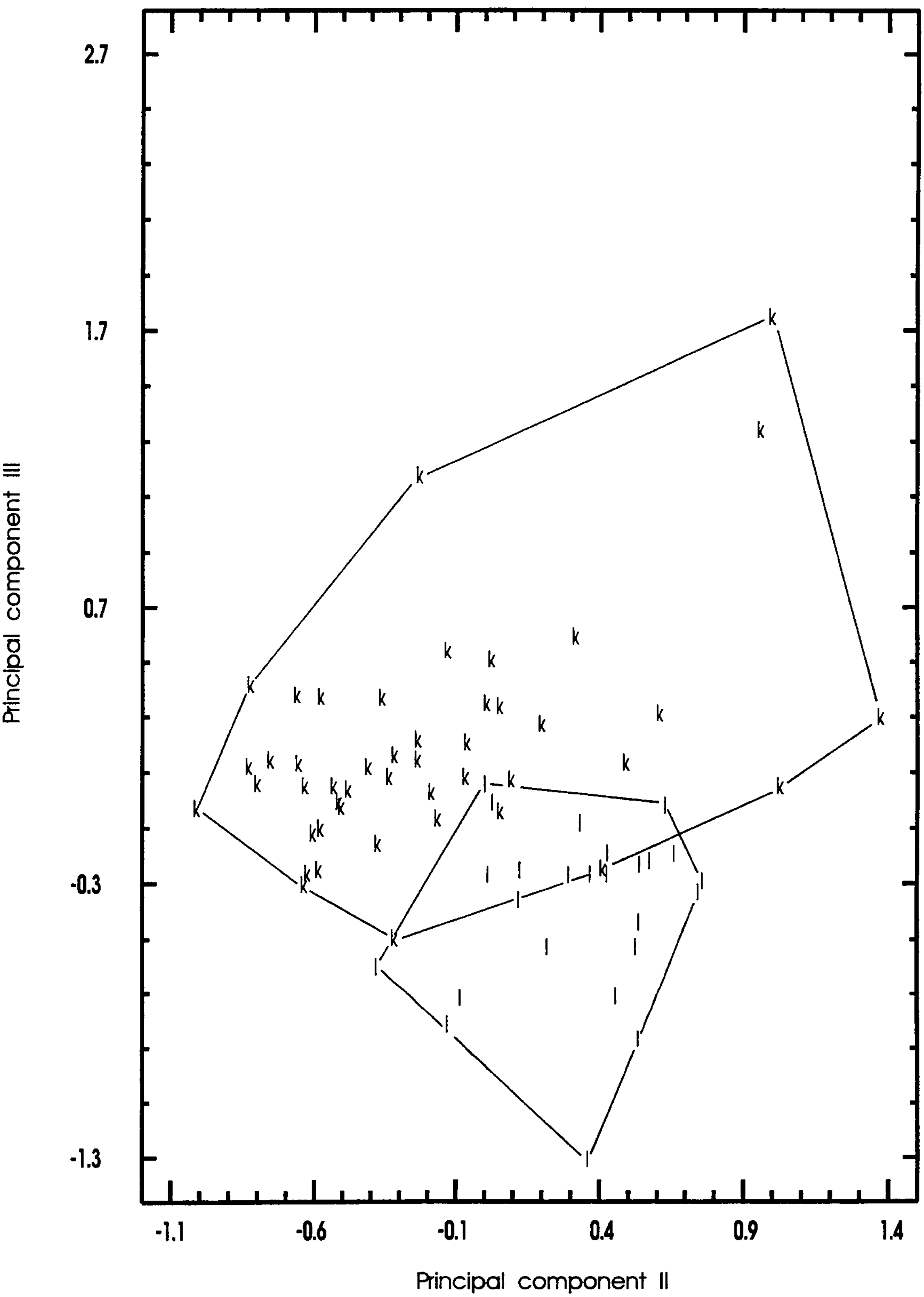


Fig. 48. Principal component analysis for selected morphometric characters for G. kongi (k) and G. latifrons (l).

A PCA of meristic data using D2, A, CV, PCV, P1, UGR, LGR, UPPCR, and LPCR, also suggested two groups, with some overlap (Fig. 49). A discriminant analysis using all morphometric characters correctly separated all G. kongi, and all but one (96.0 %) G. latifrons, which is not the unpigmented-mouth specimen from the Indian Ocean. Markle and Meléndez (1989) suggested a population-level differentiation of G. kongi off Chile, a difference supported by the newer data (Table 12).

Guttigadus kongi differs from G. nudicephalum in having more anal fin rays (61-75 vs 56-60) and more gill rakers in the upper and lower limbs (6-10 vs 3-5 and 13-21 vs 10 -11, respectively).

Material examined: FAKU 348 (1,144 mm SL), Eastern South Pacific, localities unknown. FAKU 863 (1, tail broken), Eastern South Pacific, localities unknown. FAKU 957 (1, 118 mm SL), Eastern South Pacific, localities unknown. ISH 277/78 (8, 78-158 mm SL), 43°48'S, 59°32'W, 520-570 m, 22 June 1978. ISH 1227/66 (1, 126 mm SL), 39°56'S, 55°58'W, 600 m, 19 June 1966. LACM 44318-1 paratypes (3, 131-135 mm SL. (same data as holotype). MNHNC P6438 (holotype, 147 mm SL), Eastern South Pacific, 34°51'S, 72°36'W, 690 m, 30 Aug. 1980. MNHNC P6436 paratypes (1, 157 mm SL), 34°00'S, 72°14'W, 880 m, 31 Aug. 1980. MNHNC P6437 (paratypes 2, 144-145 mm SL), 27°06'S, 71°02'W, 800 m, 18 Jan 1981. MNHNC P6573 (paratypes 5, 108-153 mm SL), 42°50'S, 75°00'W, 481 m, 17 Sept. 1977. MNHNC P6574 (paratype 1, 112 mm SL), 37°45'S, 73°55'W, 714 m, 22 Aug. 1981. MNHNC P6589 (cleared and stained). MSU uncat. (1, 105 mm SL), 53°50S, 140°40'W, 320-550 m, 20 V 1980. MSU uncat. (1, 79 mm SL), 42°38'S, 01°34'W, 720-740 m, 10 X 1979. MSU P13664 (2, 200-201 mm SL), 42°33'S, 58°14'W, 1400 m, 6 VIII 1974. MSU P13657 (1, 212 mm SL), 52°07'S, 55°02'W, 1500 m, 20 VIII 1974. MSU P16042 (3, 121-132 mm SL), 45°00'S, 59°50'W, 650-850 m, 10 VIII 1974. MSU P16041 (4, 120 mm SL + not good shape), 55°53'S, 143°39'W, 780-800 m, 25 V 1980. MSU 13677 (3, 94-116 mm SL), 41°56'S, 57°31'W, 830-710 m, 5 VIII 1974. MSU 16503 (1, 92 mm SL), 47°19'S, 148°22'E, 27 IV 1983. MSU uncat. (1, 157 mm Sl), 42°11'S, 00°4'W. NMNZ P23396 (1, 57 mm Sl), 42°56'S, 176°05'W, 800-810 m, 12 IX 1988. NMNZ

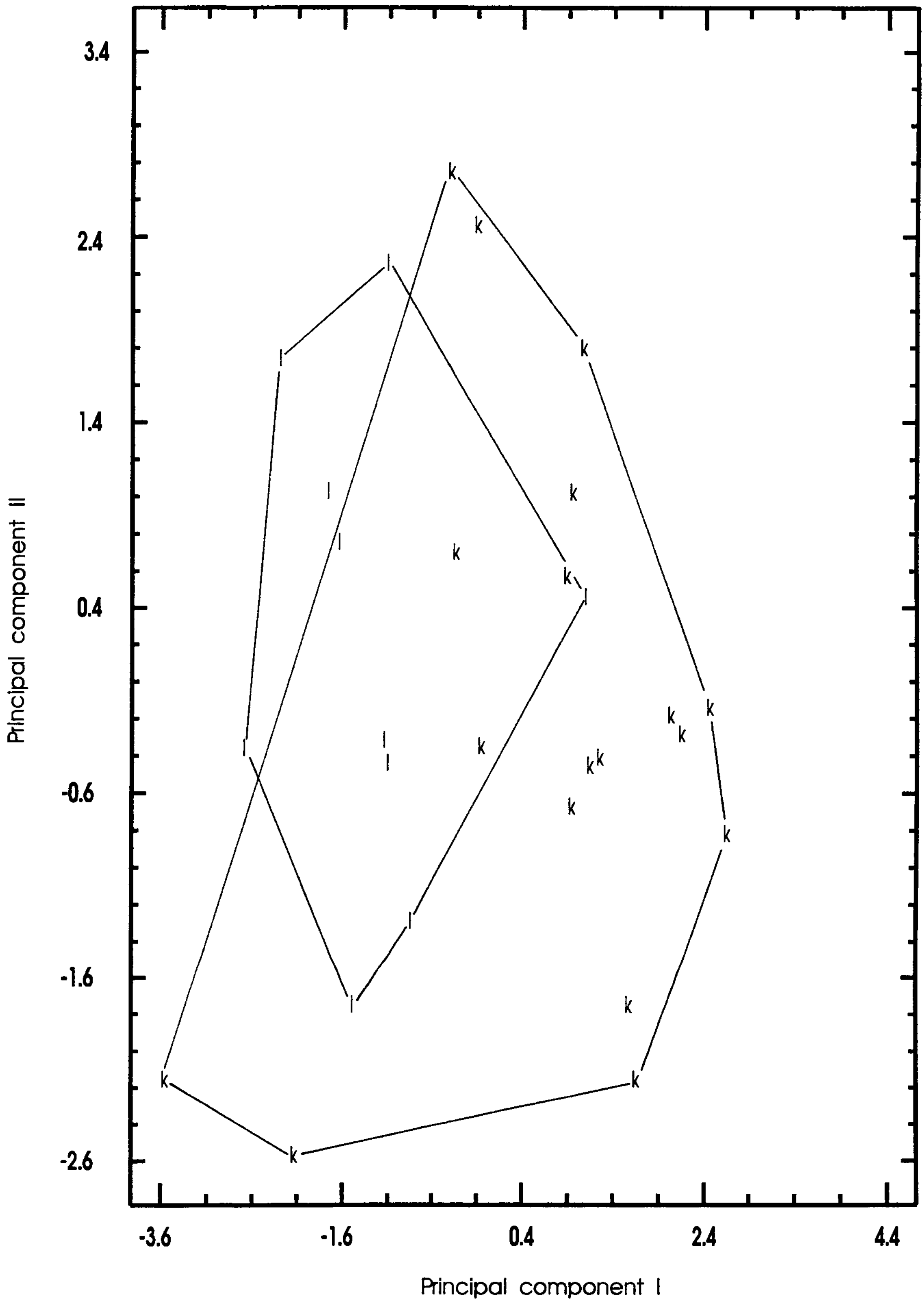


Fig. 49. Principal component analysis for meristic characters for G. kongi (k) and G. latifrons (l).

Table 12.- Comparison between selected meristic characters of <u>Guttigadus</u> <u>kongi</u> from Southwestern Pacific, Southeastern Pacific and Southern Atlantic

	D1				D2																
	4	5	6	7	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
SW Pacific		3	5						1	1	1		1	1	1						
SE Pacific	4	10	2				1	1		2	2	1	2	2	2						
S Atlantic		3	12	3	1			1	2	1	1	1	2	3		1	1	1			1

	A															PCV			
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	10	11	12	13
SW Pacific			1	2		1	1	2										8	
SE Pacific		3	2	2	3	1		2									11	3	
S. Atlantic	1		2	5	2	2	1			2	2			1	1	1	5	8	5

	CV								TV								P1					
	37	38	39	40	41	42	43	44	49	50	51	52	53	54	55	56	22	23	24	25	26	27
SW Pacific		1	4	1	1					1	4	1	1					1	2	2	2	1
SE Pacific				1	1	7	4					2	5	6			5	7	7	1		
S. Atlantic	1	4	6	6	1		1	1	1	4	7	3	1			2	1	1	10	6	4	

	LGR									UGR					TGR*								
	13	14	15	16	17	18	19	20	21	6	7	8	9	10	20	21	22	23	24	25	26	27	29
SW Pacific	1	3	2	1	1					2	4	1	1		2	1	1			2			
SE Pacific				4	6	6	1	1	1			2	13	4	1	1			1	3	6	6	1
S. Atlantic	2	1	10	3	1	3		1	1	6	13	3			2	2	9	2	3				

* added 30 & 31 total vertebrae both with one individual in SE Pacific.

P14852 (1, 73 mm SL), 44°45'S, 173°38'E, 900 m. NMNZ P20300 (1, 156 mm SL), 44°34'S, 176°42'E, 1070 m. NMNZ P.9545 (1, 68 mm SL), off New Zealand, western South Pacific. RUSI 27490 (1, 86.7 mm SL), 46° 40'S, 37° 51'E. USNM 283119 (paratypes 3, 125-165 mm SL), (same data as holotype). ZIL uncat. (1, 157 mm SL), Chatham Ridge, eastern New Zealand. ZIL uncat. (1, 118 mm SL), 55°01'S, 128°50'W, 410-500 m, 22 XII 1972.

Other material examined of G. kongi but not included in the analysis: USNM 304646 (1), 46° 00'S, 83° 58'W. 9 X 1966. USNM 304624 (8), 32° 08'S, 71° 43'W, 960 m, 12 VII 1966. USNM 304556 (2), 35° 26'S, 73° 01'W, 290 m, 9 VIII 1966.

Guttigadus latifrons (Holt and Byrne, 1908)

(Fig. 50)

Laemonema latifrons Holt and Byrne, 1908:31-36.

Laemonema latifrons: Rass, 1954 :8. Parin,1984:57. Matallanas,1985: 289-290. Cohen,1986: 717. Biscoito and Maul,1989: 1. Markle and Meléndez, 1989: 875. Cohen et al. 1990: 361.

Diagnosis: Body short and moderately deep; covered by small and deciduous scales; ending in small and thin caudal peduncle; 51-61 total vertebrae; mouth floor, gill chambers, and lips dark; modified scales on lateral line ca. 21-25.

Description: Head 23.7 -27.3 % SL; mouth subterminal, slightly inclined. Snout short, 6.6-8.2 % SL. Maxillary with an external row of conspicuous canine-like teeth; two rows inner of small villiform teeth. Dentary with one row of canine-like teeth; two patches with large teeth near symphysis. Teeth on vomer canine-like, in a rounded patch. Barbel on chin 1.9-3.9 % SL., smaller than orbit diameter. Orbit diameter, 5.7-8.2 % SL. Interorbital width 7.7-10.4 %

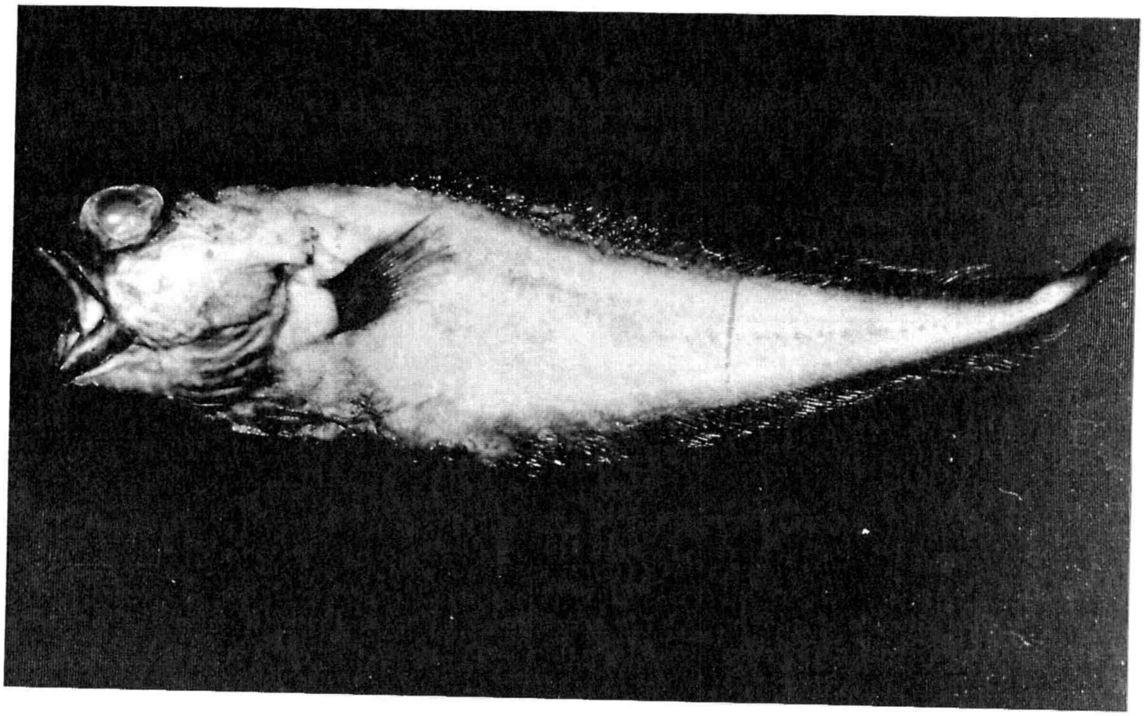


Fig. 50. Guttigadus latifrons (Holt and Byrne, 1908)
ISH 787/74 (149 mm SL)

SL, somewhat larger than orbit diameter. Upper jaws 10.3-13.2 % SL, ending at about same vertical as posterior end of pupil. Upper border of opercle bone continuous. Postorbital length 11.6-13.5 % SL.

Greatest depth of body around area of anus or between anus and insertion of pelvic fin, 16.3-27.1 % SL. Depth at first anal ray 16.9-24.7 % SL. Anus and anal fin separated by a distance twice or larger than height of caudal peduncle. Preanus length 29.5-38.8 % SL. Preanal length 34.7-43.9 % SL. Predorsal length 25.5-30.4 % SL. Depth at anus 16.3-26.7 % SL. Caudal peduncle depth 1.8-3.1 % SL.

First dorsal fin with 5-6 rays (X= 5.6 mode= 6 cv= 9.2); base short 2.6-4.0 % SL; first ray almost buried beneath skin; third ray longest, 5.3-12.2 % SL., higher than caudal depth in well-preserved specimens, remaining rays slightly decrease in height. Second dorsal fin with 64-76 rays (X= 70.3, mode= 72, cv= 5.4); long base, 61.6-67.1 % SL, ray length gradually decreases from beginning to end of fin. Anal fin with 61-76 rays (X= 68.9, mode= 66, cv= 5.7), shorter than second dorsal fin, 53.8-63.4 % SL. Pectoral fin with 21-26 rays (X= 22.2, mode= 23, cv= 5.4); its base 4.1-4.9 % SL; prepectoral length 22.9-28.4 % SL. Pelvic fin with three rays, exterior two longest; length 14.9-24.5 % SL; rays reaching the anus. Caudal fin asymmetrical, 12-14 lower procurrent rays (X= 12.9, mode= 13, cv= 4.7) almost equal or slightly greater than upper procurrent rays, 10-12 (X= 10.8, mode= 11, cv= 5.6), principal rays 6 (X= 5.8, mode= 6) (one specimen with 5 rays). Total vertebrae 54-61 (X= 57.9, mode= 58, cv= 3.0), precaudal vertebrae 10-13 (X= 11.8, mode= 12, cv= 6.8), caudal vertebrae 41-49 (X= 46.0, mode= 47, cv= 4.0). Gill rakers 7-8 + 14-17, total= 21-25. Lateral line with 21-25 scales modified; scales on an straight line about 145-150. Scales above lateral line 14, below lateral line 38.

Color in alcohol: Body mainly dark grey to light brown. Vertical fins are dark, as is the caudal fin. Lips, floor and roof of mouth, and gill chambers are dark. Juveniles have seven or eight, thin bluish vertical bands and retain them at larger sizes than _G_. _kongi_. Bars are present in ISH 13/82 (83 mm SL) from northwestern Atlantic, PPSIO uncataloged (82.1-114 mm SL) from Indian Ocean, and light bars in a specimen from Mediterranean Sea, off Spain, ICM uncataloged (182, mm SL).

Distribution: _Guttigadus_ _latifrons_ is reported from the eastern North Atlantic, Mediterranean, southwestern Atlantic (Holt and Byrne 1908, Matallanas 1985, Markle and Meléndez 1989) and western Indian Ocean (PPSIO uncat). Markle and Meléndez (1989) indicated that the southwestern Atlantic locality might have been due to a mix-up of samples. However, correspondence with ISH curator, M. Stehmann, plus a new record from the Indian Ocean suggest that the species is more widely distributed that previously thought, and that the southwestern Atlantic record is valid. The species lives in continental slope depths from 770-1875 m (Fig. 43).

Comments: The two syntypes of this species are lost (O'Riordan, personal communication). We found little meristic differentiation between populations from the eastern North Atlantic and Indian Ocean, except in caudal and total vertebral counts (Table 13).

Guttigadus latifrons is very similar to G. kongi and G. globosus (see above). The dark-mouth forms, G. latifrons and G. globosus, appear to be allopatric sister species (Figs. 42, 44), and are the deepest-living members of the genus. Guttigadus latifrons differs from G. nudicephalum in having more second dorsal fin rays (64-76 vs 59-62), more anal fin rays (61-76 vs 56-60), fewer pectoral fin rays (21-26 vs 27-28), more caudal vertebrae (41-49 vs 36-38), and more upper and lower gill rakers (7-8 vs 3-5 and 14-17 vs 10-11).

Material examined: ICM (Barcelona, Spain) uncat. (1, 182 mm SL), 40°20'-25'N, 1°53'-56'W' off Barcelona, Spain, 1715-1753 m, 3 VIII 1987. IOS 51021 (1, 108 mm SL), 49° 38'N, 12° 40'W, 1860-1875 m, 9 V 1981. IOS 51022 (2, 105-121 mm Sl), 49° 33'N, 12° 38'W, 1575-1600 m, 9 V 1981. IOS 51305 (1, 100 mm SL), 51° 50'N, 13° 05'W, 1005-965 m, 18 II 1982. IOS 9752 #1 (8, 92-140 mm SL), 51° 16'N, 11° 42'W, 1007-1042 m, 7 IV 1978. ISH 735/74 (1, 109 mm SL), 60°44'N, 12°41'W, 770-806 m, 26 XI 1974. ISH 738/74 (1, 4, 126-209 mm SL), 60°41'N, 13°00'W, 980-1000 m, 26 XI 1974. ISH 787/74 (1, 149 mm SL), 53°46'N, 13°56'W, 850-900 m, 5 XII 1974. ISH 5013/79 (1, 142 mm SL), 59°13'N, 9°42'W, 980 m, 11 VI 1979. ISH 30/81 (1, 139 mm SL), 60°20'N, 10°40'W, 798-808 m, 26 IX 1981. MSU uncat. (1, 106 mm SL), R/V Vityaz, sta 2673. MSU uncat. (cleared and stained) North eastern Atlantic. PPSIO uncat. (4, 82-114 mm SL), 25°09'S, 35°36'E, 890-1000 m, 25/26 XI 1988. PPSIO uncat. (1, 88 mm SL), 25°12'S, 35°04'E, 23 XI 1988.

Table 13.- Comparison between selected meristic characters of *Guttigadus latifrons* from Nortwestern Atlantic and Indian Ocean

	D1		D2												
	5	6	64	65	66	67	68	69	70	71	72	73	74	75	76
Northwestern Atlantic	8	12		1	1	3	2	1			4	1	2	1	2
Indian Ocean	5	1	1				1		1			1		1	

	A															
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76
Northwestern Atlantic			1			3	3		1	2		2	3	1		1
Indian Ocean	1			2					2					1		

	PCV				CV								
	10	11	12	13	41	42	43	44	45	46	47	48	49
Northwestern Atlantic	1	6	10	4					2	6	7	4	1
Indian Ocean		1	3	2	1	1		3	1				

	TV								P1						LGR			
	54	55	56	57	58	59	60	61	21	22	23	24	25	26	14	15	16	17
Northwestern Atlantic				3	7	5	3	2	7	5	6				1	5	5	5
Indian Ocean	1	1	4						1	2	2			1		2	4	

	UGR		UPC			LPC		
	7	8	10	11	12	12	13	14
Northwestern Atlantic	10	6	1	3	1	2	2	1
Indian Ocean	6		1	4		1	4	

Guttigadus nana (Taki, 1953)

(Fig. 51)

Laemonema (Guttigadus) nana Taki,1953:201-210.

Laemonema nana: Okiyama, 1986, 321-333 (Larval stages). Okamura, 1984:91, Parin,1984:57. Markle and Meléndez, 1989: 875. Cohen et al. 1990 (list).

Diagnosis: A dwarf species (maximum size 73.1 mm SL) with short, slightly deep body, covered by small, deciduous scales; body ending in a narrow caudal peduncle; upper gillrakers 1-2; interorbital width 5.2-7.1 % SL, equal to or shorter than orbit diameter (6.3-7.4 % SL); vomer toothless; caudal vertebrae 27-30; anal fin rays 46-53.

Description: Head 23.3-26.0 % SL; mouth subterminal to terminal, slightly inclined. Snout short, 5.6-6.9 % SL. Maxillary and dentary with three or more rows of small canine-like teeth. Vomer toothless. Barbel on chin, 4.4-6.4 % SL, equal to or smaller than orbit diameter. Orbit small, 6.3-7.4 % SL, at least four times in head length. Interorbital narrow 5.2-7.1 % SL, almost four times in head length, slightly shorter than orbit diameter. Maxillary 10.9-12.9 % SL, ending at about same vertical as end of pupil. Opercle bone border continuous along upper portion. Postorbital length 12.8-14.8 % SL. A conspicuous whitish area behind orbit, where gas bladder connected with skin.

Greatest depth of body between anus and insertion of pelvic fin, 15.6-21.1 % SL. Depth at anus 15.6-19.8 % SL. Depth at first anal ray 16.2-19.8 % SL. Anus and anal fin

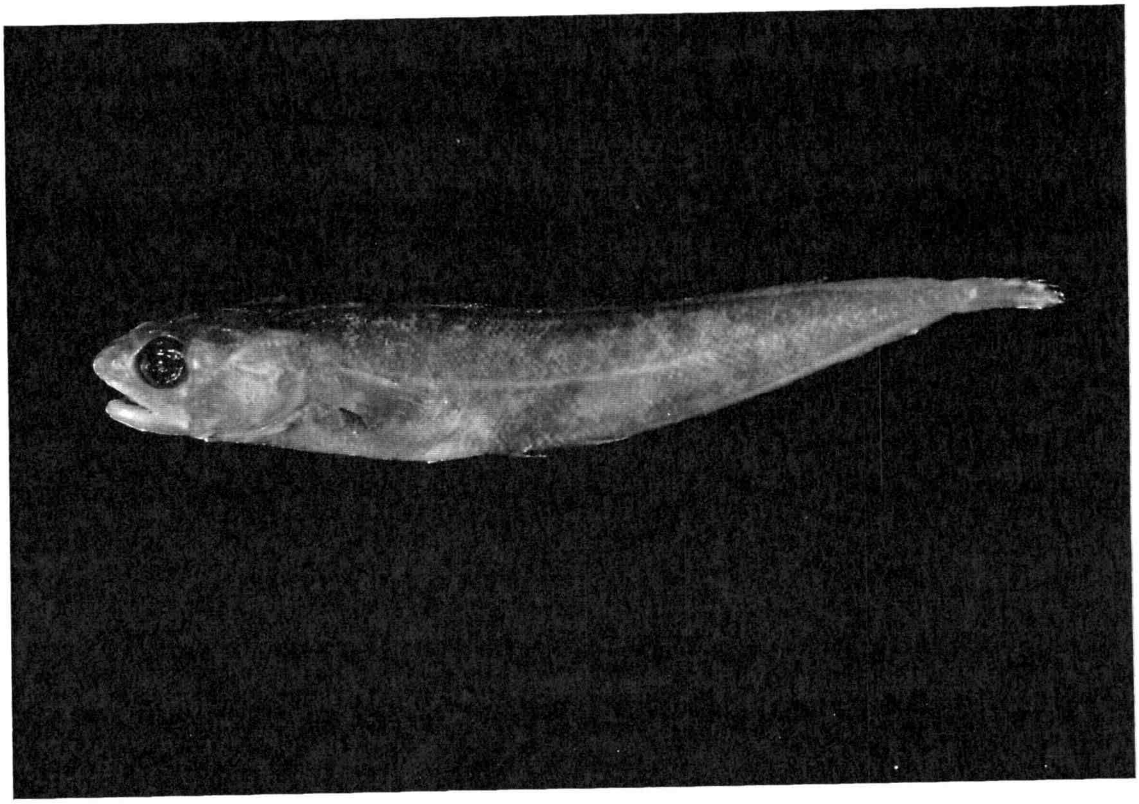


Fig. 51. Guttigadus nana (Taki, 1953)
UMMZ 214588 (73.1 mm SL)

not separated. Preanus length 31.6-42.2 % SL. Preanal length 34.7-43.8 % SL. Predorsal length 27.7-32.2 % SL. Caudal peduncle depth 3.2-4.2 % SL.

First dorsal fin with 4-6 rays (X= 5.1 mode= 5 cv= 10.6); short base 5.0-6.6 % SL; first ray shortest, third ray longest, 3.5-11.7 % SL, longer than caudal depth in well-preserved specimens; remaining rays decrease slightly in height. Second dorsal fin with 45-54 rays (X= 47.6 mode= 47, cv= 5.1); base large, 56.2-62.3 % SL; ray height gradually decreases from beginning to end. Anal fin with 46-53 rays (X= 48.2, mode= 47, cv= 4.2), shorter than second dorsal fin 47.0-59.6 % SL. Pectoral fin with 22-24 rays (X= 23.2, mode= 23, cv= 2.4), its base 5.2-5.8 % SL; prepectoral length 25.6-28.1 % SL. Pelvic fin with three rays, exterior two longest, length 15.0-17.2 % SL, but not reaching vent. Caudal fin asymmetrical, 9-10 lower procurrent rays (X= 9.5, mode= 10, cv= 5.5), almost equal to or slightly greater than upper procurrent rays, 7-8 (X= 7.5, mode= 8, cv= 7.0), principal rays 6 (X= 5.9, mode= 5.9) (one specimen with 5 rays). Total vertebrae 39-41 (X= 39.7, mode= 40, cv= 1.7), precaudal vertebrae 10-12 (X= 11.1, mode= 11, cv= 5.4), caudal vertebrae 27-30 (X= 28.6, mode= 29, cv= 2.9). Gill rakers 2-1 + 6-4, total= 5-8. Lateral line with 60-75 scales on an straight line. Scales above lateral line 8 (X= 8, mode= 8, cv=5.2).

Color in alcohol: Body light brown, fins almost transparent. A white semi-circle in upper operculum area, where anterior part or cornua of gas bladder connected to skin.

Distribution: Only known from waters off Japan (Fig. 43) in very shallow water (50-60 m).

Comments: Guttigadus nana is the smallest (42.3-73.1 mm SL) and shallowest-living member of the Laemonema-Guttigadus group. It also has the lowest number of rays in the second dorsal and anal fins, and lowest number of caudal vertebrae (27-30). Taki (1953) erected a subgenus Guttigadus based on its small size, presence of sensory papillae on lateral line, reduced gill rakers, low number of rays in second dorsal and anal fins, and low number of vertebrae. The material we examined included sexually mature females, which suggests that Guttigadus nana is paedomorphic. The process of paedomorphosis in this species appears to involve mostly reductions in serially repeating structures, including vertebrae, vertical fin rays procurrent caudal rays, and gill rakers in the upper arch (Table 3). Guttigadus nana showed the deletion of pharyngobranchials 1 and 2. The absence of pharyngobranchial 2 (Fig. 5a) might also reflect this reductionist developmental program and suggests that pharyngobranchial 2 might be a late-forming element. Related to pharyngobranchial 1, there are the absence of the uncinate process, interarcual ligament, and interarcual cartilage (Fig. 5a). Absence of the vomer and the neck on the gas bladder (Fig. 7e) might also reflect reductionism, as does the absence of a laminar bone on the first pterygiophore of the first dorsal fin (Fig. 11c). Although a reduction in structures is a trend in modern fishes, it is important point to mention in order to explain the probable paedomorphic or neotenic condition of G. nana.

Two larvae (4.1 and 11.3 mm SL) were described by Okiyama (1986). The largest specimen had developed all fin rays whereas the smallest had not. The series of sensory pits on the opercle were also developed on the largest specimen. Both were lightly pigmented.

Material examined: BSKU 42415 (1, 58 mm SL), 33° 24′N, 133° 35′E, 60 m. 6 XI 1985. BSKU 42416 (1, 53 mm SL), (same as BSKU 42415). UMMZ 212836 (1, 57.3 mm SL), Vicinity of Miski, Sagami, Japan, 1929. UMMZ 214587 (1, 68.1 mm SL), collection Dr. Ichiro Kanko, Nagasaki, Japan. 16 VII 1929. UMMZ 214588 (6, 51.2-73.1 mm SL), (one clear and stain) Japan. USNM 273285 (1, 42.3 mm SL), Japan, 50 m, 20 II 1975.

Guttigadus nudicephalum (Trunov, 1990)

(Fig. 52)

Paralaemonema nudicephalum Trunov, 1990:81-83.

Diagnosis: Body short, ending in narrow caudal peduncle; head large scaleless; gill rakers 3-5 + 10-11; vomer triangular; modified scales on lateral line ca. 14-15.

Description: Head length 27.3-31.1 % SL. Mouth subterminal, maxillary 13.0-15.0 % SL, one outer row of strong caniniform teeth and one inner row of small teeth that does not continue to end of maxillary. Dentary with teeth pattern similar to that in maxillary. Vomer triangular, with small teeth. Barbel on chin 3.5-4.2 % SL. Orbit diameter 7.5-9.5 %

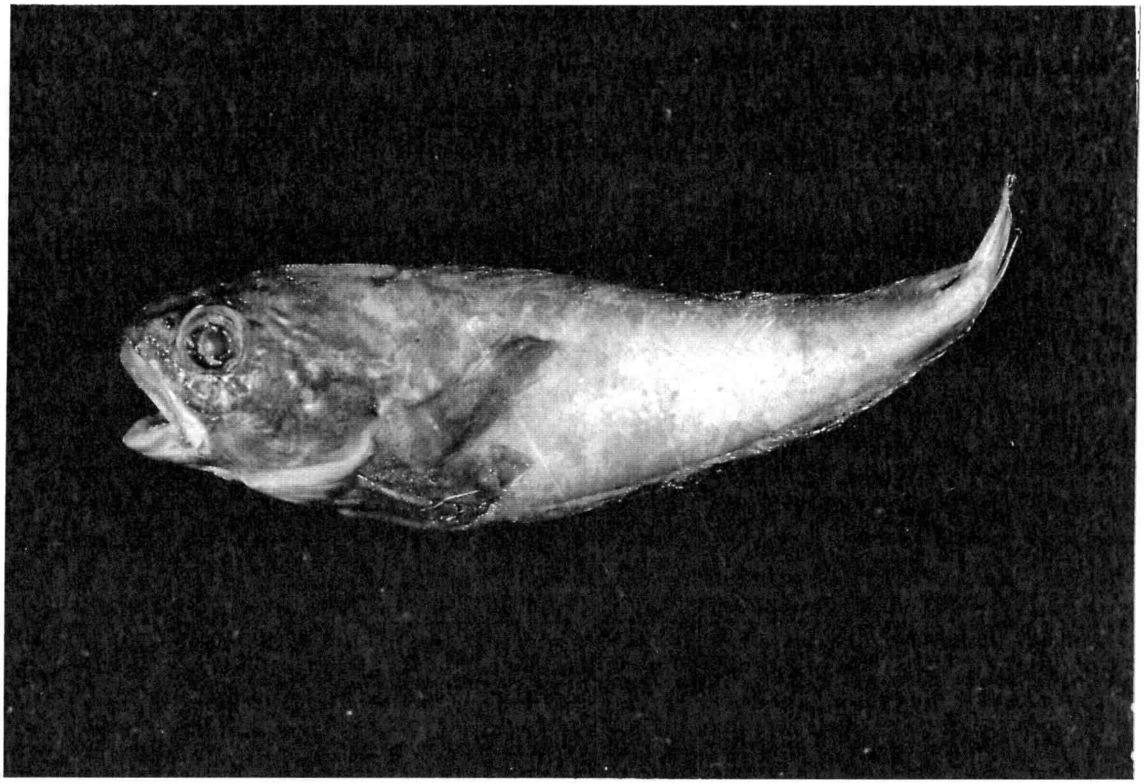


Fig. 52. Guttigadus nudicephalum (Trunov, 1990)
PPSIO uncataloged (82 mm SL)

SL, smaller than interorbital width, 8.9-11.3 % SL. Postorbital length 14.8-16.7 % SL.

Predorsal length 30.5-33.6 % SL. Anus separated from anal fin; preanus length 40.3-47.5 % SL; preanal length 43.0-51.0 % SL. Pectoral fin insertion behind insertion offirst dorsal fin; prepectoral length 32.3-34.3 % SL. Prepelvic length 27.1-31.9 % SL.

First dorsal fin with 4-5 rays (X= 4.2, mode= 4, cv= 10.6), second ray longest 6.1-8.5 % SL. Second dorsal fin with 59-62 rays (X= 60.2, mode= 60, cv= 1.8), its base 58.3-60.6 % SL. Anal fin with 56-60 rays (X=57, mode= 56, cv= 3.0), its base 51.7-55.0 % SL, last rays almost reaching last rays of second dorsal fin. Pectoral fin with 27-28 rays, its base 7.1-8.8 % SL, its length 15.8-20.5 % SL. Pelvic fin with two large and two shorter rays, its length 23.8-29.1 % SL. Total vertebrae 48-51 (X= 49.6, mode= 50, cv= 2.3), precaudal vertebrae 12-13 (X=12.6, mode= 13, cv= 4.3), caudal vertebrae 36-38 (X= 37, mode= 37, cv= 1.9). Caudal fin slightly asymmetrical, upper procurrent rays 11-12 (X= 11.2, mode= 11, cv= 3.9), principal rays 6, lower procurrent rays 12-14 (X= 13.2, mode= 14, cv= 6.3). Gill rakers 3-5 + 10-11, total= 13-15. Modified scales on lateral line 14-15; lateral body scales about 114-135. Scales above lateral line 18-20 (X=19.3, mode= 20, cv= 4.9), scales below 40-55 (X= 47.5, mode= 40, cv= 15.9).

Color in alcohol: Body light yellow to yellowish, visceral area gray; all fins dark, most of head brown, except in area of branchiostegal membranes; a conspicuous brown spot between pelvic fins.

Distribution: This species is known only from the Indian Ocean from 24°54'S, 6° 25'E (Whale Ridge) to 25° 09'S, 35° 36'E (Fig. 45), at depths of 630-680 m (Trunov 1990). Our data expand the depth range to 1000m.

Comments: Guttigadus nudicephalum is very distinctive from other Guttigadus in its low dorsal fin ray and vertebral counts (Table 3 and above comparisons).

Material examined: MSU uncat. (2, 84-96 mm SL), R/V Vityaz, Indian Ocean, (one cleared and stained). PPSIO uncat. (3, 78-104 mm SL), 25°09'S, 35°36'E, 890-1000 m, 24-25 XI 1988.

Species *incertae sedis*

Guttigadus nudirostre (Trunov, 1990)

Paralaemonema nudirostre Trunov, 1990:81-83.

Paralaemonema nudirostretira, (*lapsus*), Trunov, 1990:81-83.

Description: (from original paper) D1 4- 6, predominantly 5; D2 63-74; A 63-70; P1 24-25, most often 25; P2 4-5, very rarely 5; gill rakers 6-7 + 13-18, scales on lateral line 21-25; scales on a transverse series 120-140; pyloric caeca 7-11; total vertebrae 12 + 41. Predorsal length 28.8-32.0 % SL; preanal length 42.4-47.0 % SL, maxillary 12.2-14.8; orbit diameter 6.9-8.3 % SL; interorbital length 10.1-11.6 % SL. Base color of body cinnamon brown with brownish tinge. Walls of anterior mouth and gill cavities, gill filaments, and pyloric caeca light, inner region of mouth and gill cavities (toward throat and bases of gill arches) darkish blue.

Holotype: ZIN 48159 (189 mm SL), 42°05'S, 1°21'E, 800 m, 3 April 1981. Paratypes: ZIN 48159 (3, 167-183 mm SL), same data as holotype. ZIN 48160 (2, 147-203 mm SL), 42°03'S, 0°11'E, 550-580 m, 28 July 1976. ZIN 48161 (2, 147-158 mm SL), 41°52'S, 0°18'E, 500-525 m, 29 July 1976.

Distribution: The species is known only from the Discovery Seamount, where it was collected at depth of 500-800 m.

Comments: This species is similar to *G. kongi* and *G. latifrons*, and shares the light mouth pigmentation and the bathymetric range of *G. kongi*. According to the original description of *G. nudirostre*, it has fewer lateral body scales (120-140) than *G. kongi* (*ca*. 170). We treat this species as *incertae sedis*, suspecting it to be a junior synonym of *G. kongi*.

Guttigadus squamirostre (Trunov, 1990)

Paralaemonema squamirostre Trunov, 1990:81-83.

Description: (from original paper) D1 4; D2 64; P1 24; P2 5; gill rakers 8 + 16, scales above lateral line about 26; transverse series about 160. Predorsal length 27.1 % SL; preanal length 37.3 % SL, orbit diameter 8.2 % SL; interorbital width 8.8 % SL. Body brownish cinnamon. Mouth and gill cavities (apart from darkish blue region around throat and near bases of gill arches), gill arches and rakers light cinnamon brown.

Holotype: ZIN 48157 (161 mm SL), 31°20'S, 15°51'E, 517 m, 24 August 1976.

Distribution: Off the southwestern coast of Africa at a depth of 517 m.

Comments: This species is also similar to G. kongi and G. latifrons, and again shares the light mouth pigmentation and bathymetric range of G. kongi. Trunov reports approximately 23 scales above the lateral line in G. squamirostre, almost double our counts in G. kongi (12). This difference in squamation suggests the existence of another species.

Laemonemodes compressicauda Gilchrist, 1903

Laemonemodes compressicauda Gilchrist, 1903: 208-209.

Comments: Laemonemodes compressicauda Gilchrist (1903) was based on an approximately 60 mm SL individual from the east coast of South Africa which may have been loaned to the British Museum, but which is apparently lost (P. A. Hulley, South African Museum, pers. comm. 23 June 1988 and J. Chambers, British Museum Natural History, pers. comm. 16 October 1989). Unfortunately, the reported low second dorsal fin (46) and anal fin ray (46) counts most closely resemble G. nana. It seems unlikely that the shallow-living G. nana from Japan is conspecific with the deep-living (550-735 m)

L. compressicauda from South Africa and we are obliged to treat the latter as *incertae sedis*.

ZOOGEOGRAPHY

Howes (1990) pointed out that gadoids, including morids, have a marginal oceanic distribution, following continental margins or sea mountain chains. Laemonema has a worldwide distribution, except for the Northeastern Pacific Ocean and eastern Indian Ocean. It occurs from 60° N to 40° S, is most abundant at approximately 200-600 m depth, and reaches its greatest diversity in the Pacific (Fig. 53). Guttigadus is most diverse in a narrow belt, 25°S-59°S, in the Southern Hemisphere, with one species extending into the eastern North Atlantic, G. latifrons, and one western North Pacific endemic, G. nana (Fig. 54). Species of Guttigadus live deeper than Laemonema, being most abundant at approximately 600-1600 m. The zoogeography of the two genera are fundamentally different. As in many genera, Laemonema's zoogeography is dominated by the influence of anti-cyclonic gyres in the three major basins, the Atlantic, Pacific and Indian, while Guttigadus's is dominated by the circumpolar circulation of the Southern Ocean (Lutjeharms 1990).

With one possible exception, all species pairs in Laemonema (Fig. 20) are allopatric: two pairs in the Atlantic Ocean, Laemonema barbatulum plus L. yarrelli, and L. n. sp. g plus L. laureysi; and one pair in the North Pacific, L. longipes plus L. verecundum (Figs. 23 and 26). One pair, L. robustum and L. n.sp. i, might be allopatric but their distributions are unclear. Laemonema robustum

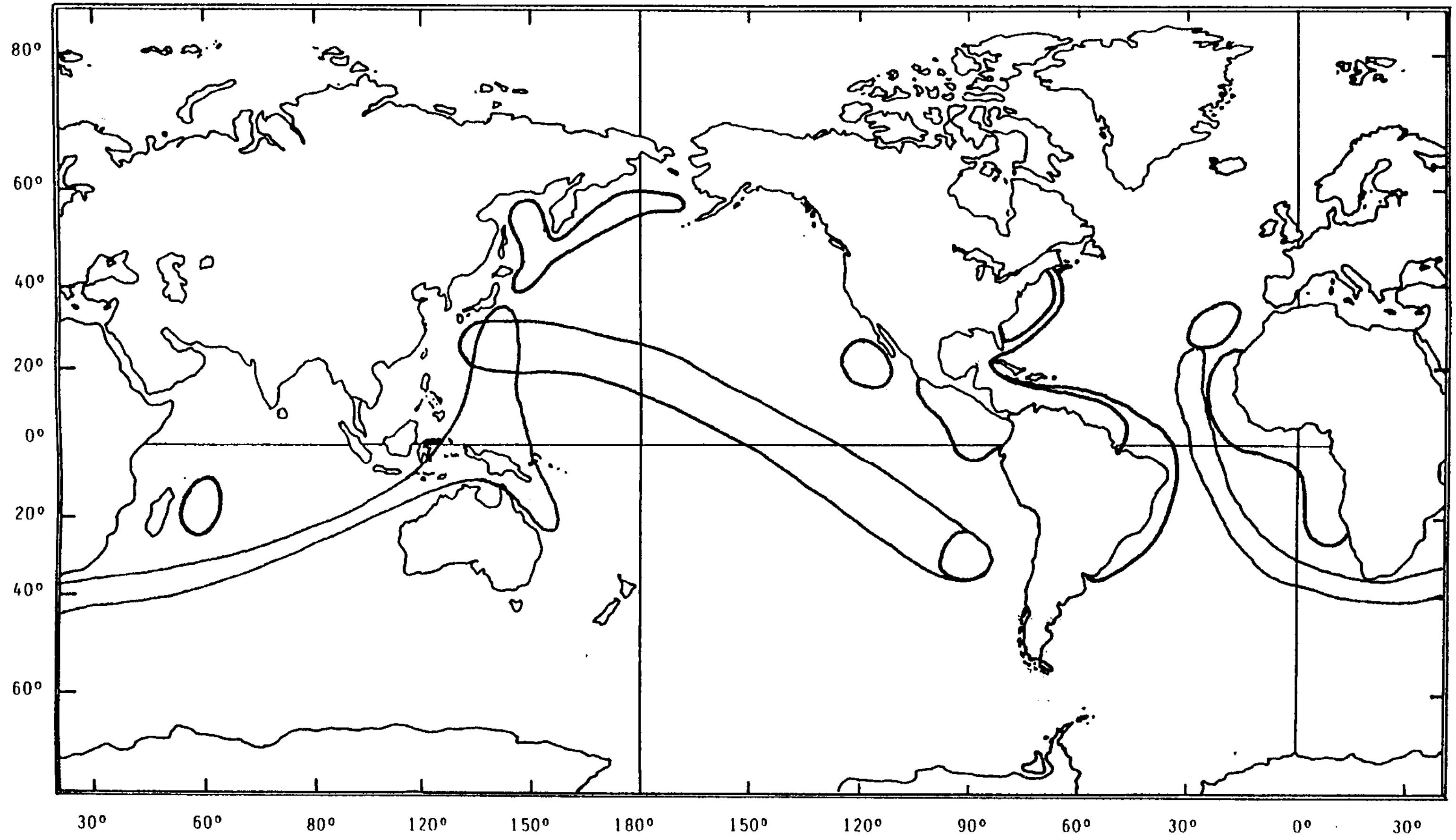


Fig. 53. Generalized distribution track of Laemonema species.

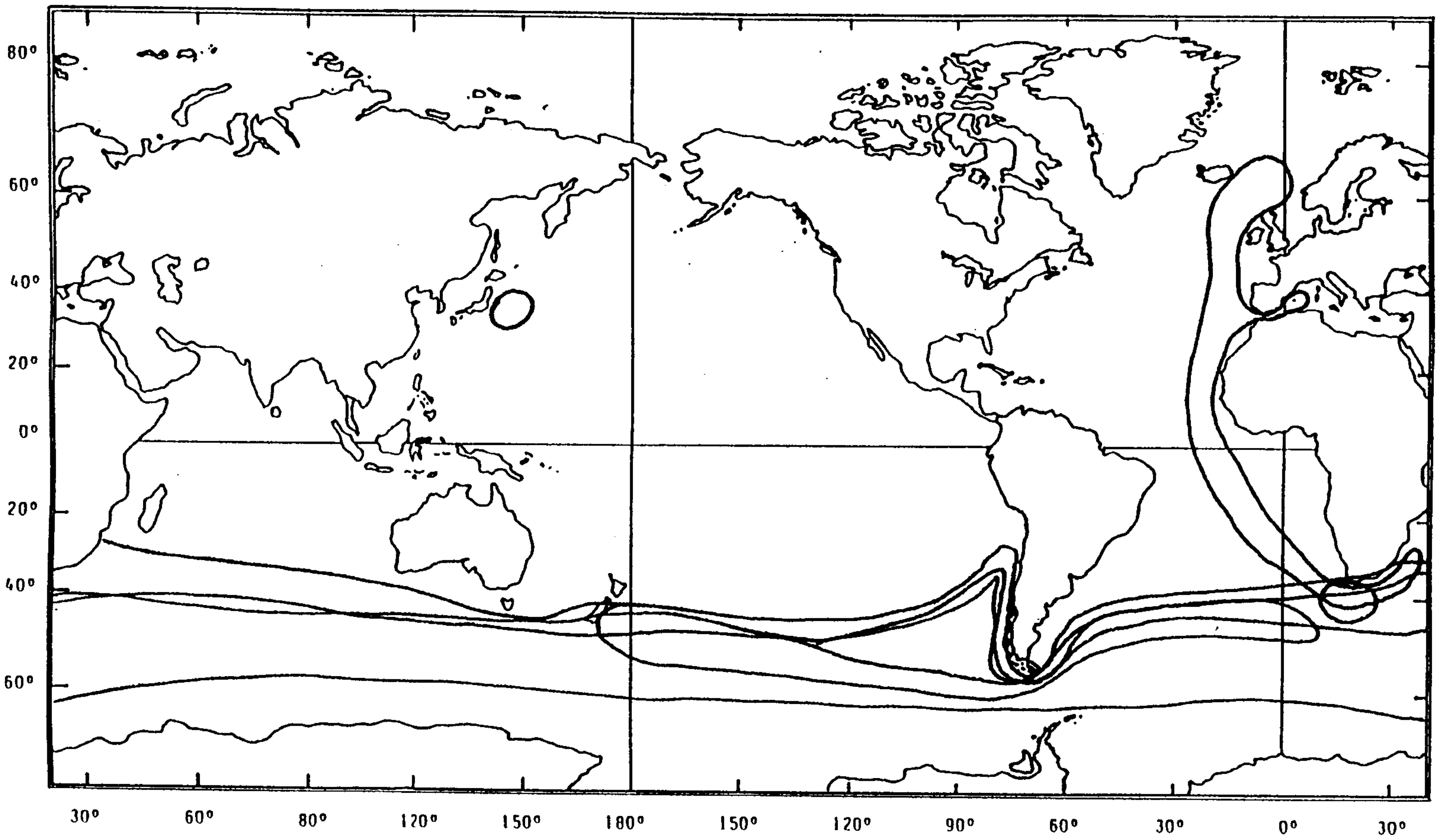


Fig. 54. Generalized distribution track of Guttigadus species.

could conceivably have the very unusual pattern across thePacific and Atlantic Oceans excluding the Indian Ocean, or be found from the eastern Atlantic through the Indian Ocean to the western Pacific (Fig. 31). In the latter case it would be partly sympatric with L. n. sp. i. (Fig. 31). All four pairs show east-west segregation. In one Atlantic pair, L. barbatulum and L. yarrelli, there may also be bathymetric segregation with L. barbatulum living over a broader and deeper range, 50-1620 m, than L. yarrelli, 220-550 m. The Pacific sister species, L. longipes and L. verecundum, also exhibit a latitudinal difference, with L. longipes in the temperate western North Pacific and L. verecundum in the tropical eastern Pacific (Fig. 23). Vicariant events associated with changes in current patterns are likely candidates for creating these patterns. For example, when the Drake Passage opened about 22 mya, the global current pattern shifted to its general pattern today (Keller 1981; Kennett 1982). These species are located on the eastern or western sides of ocean basin gyres and often restricted to subsystems such as the Kuroshio and Oyashio (L. longipes), and North Equatorial counter current (L. verecundum).

Within Laemonema the first vicariant event separated the North Pacific sister species, L. longipes and L. verecundum, from a widely distributed tropical ancestor (Fig. 53). These two clades appear to have remained largely allopatric. A number of speciation events do not result in allopatric patterns, thus requiring dispersal events, most of which are not easily discerned. For example, Laemonema rhodochir is not allopatric with the clade above it and that clade includes both Atlantic and Pacific taxa. However, at least one terminal clade provides a clear zoogeographic pattern. The eastern Pacific-Atlantic L. gracillipes clade clearly arose from a widely distributed tropical Atlantic-eastern Pacific ancestor, with the formation of the Panamanian isthmus preceding the subsequent eastern-western Atlantic separation of L. n.sp. g and L. laureysi (Figs. 26). The L. melanurum terminal clade must also have had a widely distributed ancestor. It either traversed the eastern Pacific barrier or had an eastern Pacific-Atlantic-Indo Pacific distribution.

Resolution of the problematic L. robustum distribution pattern might provide some insight regarding the L. melanurum terminal clade (Figs. 31). Laemonema robustum and L. rhodochir have the broadest latitudinal and longitudinal distribution in the genus (Figs. 23, 31). The wide distribution of L. robustum in the Pacific and Atlantic Ocean is difficult to analyze because there are few samples. With larger samples, we find no differentiation of populations in L. rhodochir (Table 8) in the Pacific Ocean. Widely distributed morids have been documented in other taxa with larger data sets, such as Antimora rostrata (Small, 1981) and Halargyreus johnsoni (Cohen et al. 1990), the latter of which has a distribution similar to L. robustum.

Guttigadus (Fig. 20) seems to have originated and evolved, mostly, in the Southern Ocean, north of the Antarctic Convergence. Miller (1993) mentions a secondary Antarctic fish fauna of midwater and near-bottom fishes belonging to World Ocean families. Guttigadus is clearly part of this fauna. Its diversity and subsequent dispersal into the northern hemisphere is some indication of the age of this fauna.

The distribution of several Guttigadus species supports Anderson's (1990) contention that many poorly known deeper living benthic species have a circumpolar distribution. However, two early vicariant events in the clade were the isolation of G. nana and G. latifrons in the Northern Hemisphere (Fig. 54). The first event, the speciation of G. nana (Fig. 20, node I), involved a bathymetric change as well as latitudinal isolation. In other members of Laemonema sensu lato, the shallowest bathymetric stage is the pelagic, "Svetovidovia"-like juvenile stage which is found in surface layers (Markle 1989). The paedomorphic morphology of G. nana (see above) is consistent with neotenic retention of the shallow water juvenile habitat. The evidence indicates that this earliest vicariant event in Guttigadus involved accelerated gonadal development in a juvenile stage (neoteny) and resulted in a unique endemic off Japan (Fig. 43).

The other latitudinal vicariant event involved the dispersal and isolation in the North Atlantic of G.

latifrons (Figs. 20 node K1 and 43) from a widely distributed Southern Ocean ancestor of G. globosus, G. kongi, and G. nudicephalum. Its South African populations presumably represent a recent re-invasion of the Southern Ocean.

Three of the remaining five Guttigadus are mostly found below 1000m with G. globiceps and G. kongi being generally shoaler. Vicariance along a bathymetric gradient would be the simplest explanation of the speciation event at node M (Fig. 20). The most interesting of this event at node M is the production of the sympatric sister taxa, G. kongi and G. globosus (Figs. 20 and 45). The shoaler-living G. kongi has a total depth range of 83-1500m, being most abundant from about 500-800m over its geographic range (Markle and Meléndez 1988). The deeper-dwelling G. globosus (1175-1600m) presumably retains the ancestral depth pattern. The circumpolar, or nearly circumpolar, distribution of G. kongi, G. globiceps and G. globosus is also seen in other outer slope fishes of the Southern Ocean (Anderson 1990, Gon and Heemstra 1990).

There is no obvious explanation for Guttigadus nudicephalum unless it represents peripheral speciation of an Indian Ocean endemic from the ancestral Southern Ocean stock. It is known only from the southern tip of South Africa (Fig. 45).

BIBLIOGRAPHY

Anderson, M. E. 1990. The origin and evolution of the Antarctic ichthyofauna. pp. 28-33. In: O. Gon and P. C. Heemstra (eds.) Fishes of the Southern Ocean. J. L. B. Smith Inst. Ich., Grahamstown, 462 pp., 12 pls.

Barbour, C.D. and B. Chernoff. 1984. Comparative morphology and morphometrics of the pescados blancos (Genus Chirostoma) from Lake Chapala, pp. 111-127. In: A. A. Echelle and I. Kornfield (eds.), Evolution of fish species flocks. University of Maine at Orono Press, 257 pp.

Baum, B.R. 1988. A simple procedure for establishing discrete characters from measurement data, applicable to cladistics. Taxon, 37(1):63-70.

Bean, T.H. 1884. Descriptions of Physiculus fulvus and Lotella maxillaris, new species of fishes collected in 1881 by the United States Fish Commission. Proceedings of the United States National Museum, 7 (16): 240-242.

Biscoito, M.J. and G.E. Maul. 1989. A new species of Laemonema from the northeastern Atlantic (Pisces : Moridae). Bocagiana. Mus. Mun. do Funchal, Madeira,127:1-8.

Chiu, T-S. 1987. Phylogeny and Zoogeography of Glytocephalines (Pisces: Pleuronectidae). Unpubl. Ph.D. dissert., Oregon State University, Corvallis, Oregon.

Chiu, T.S., D.F. Markle and R. Meléndez. 1990. Moridae. pp: 183-187. In: Fishes of the Southern Ocean. O. Gon and P. C. Heemstra (eds.). J.L.B. Smith Institute of Ichthyology, Grahamstown.

Cohen, D. M. 1973. Svetovidovia. pp: 326. In: Check list of the fishes of the North-eastern Atlantic and of the Mediterranean (Clofnan). J.C. Hureau and Th. Monod (eds.). Vol I, UNESCO, Paris.

__________. 1979. Notes on the morid fish genera Lotella and Physiculus in Japanese waters. Japanese Journal of Ichthyology, 26(3):225-230.

__________. 1986. Moridae. pp:713-723. In: Fishes of the North-eastern Atlantic and the Mediterranean. P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (eds.). Vol II, UNESCO, United Kingdom.

__________. 1990. Moridae. pp:520-523. In: Check-list of the Fishes of the Eastern Tropical Atlantic. CLOFETA II. J.C. Quéro; J.C. Hureau; C. Karrer; A. Post and L. Saldanha (eds.). Junt. Nac. Inves. Cient. e Tecnol. Lisbon, Portugal. European Icthyolo. Union, Paris, France and UNESCO,France. Vol 2:520-1080. Portugal.

Cohen, D. M., Inada, T., Iwamoto, T., Scialabba, N. 1990. FAO Species catalogue. Vol 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Fisheries Synopsis. N° 125, vol 10. Rome, FAO. 442 p.

Edwards, A.J. and C.W. Glass. 1987. The Fishes of Saint Helena Island, South Atlantic Ocean. I. The Shore Fishes. Journal of Natural History,1987,21:617-686.

Eschmeyer, W.N. 1990. Catalog of the genera of recent fishes. Published by the California Academy of Sciences. San Francisco, California. 697 pages.

Fahay, M.P. and D.F. Markle. 1984. Gadiformes: Development and Relationships, pp:265-283. In: H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall,Jr. and S.L. Richardson (eds.), Ontogeny and Systematics of Fishes, Special Publication N°1, American Society of Ichthyologist and Herpetologist, 760 pp.

Fourmanoir, P. and J. Rivaton. 1979. Poissons de la pente récifale externe de Nouvelle-Calédonie et des Nouvelles-Hébrides. Cahiers the L'Indo-Pacifique, 4:405-443.

Franz, V. 1910. Die Japonischen Knochenfische der Sammlungen Haberer und Doflein. Abhandlungen Math.-phys. Klasse K. Bayer. Akad. Wissenschaften 4, Suppl.-Bd., 1: 1-133, fig., 1-7, pls. 1-11.

Garman, S. 1899. Reports on an exploration off the west coast of México, Central and South América, and off the Galápagos Islands in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross" during 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding. XXVI. The Fishes. Mem. Mus. comp. Zool., Harvard 24: 1-431.

Gilbert, C.H. 1897. Descriptions of twenty-two new species of fishes by the steamer Albatross, of the United States Fish Commission. Proceedings of the U.S. National Museum, 19 (1115):437-457.

__________. 1905. The deep-sea fishes of Hawaiian Islands. In: The aquatic resources of the Hawaiian Islands. D.S. Jordan and B.W. Evermann (eds.). Bulletin U.S. Fish Comm., (for 1903), 22(pt.2, sect 2) pp:575-713.

Gilchrist, J.D.F. 1903. Description of New South African Fishes. Marine Investigation South Africa. 2:203-211. XVIII plates.

_______________. 1906. Description of fifteen new South African fishes, with notes on other species. Marine Investigation South Africa. 4: 143-171.

Gon, O. and P. C. Heemstra. 1990 (eds.). Fishes of the Southern Ocean. J. L. B. Smith Institute of Ichthyology, Grahamstown, 462 pp., 12 pls.

Goode ,G. B. and T.H. Bean. 1883. Reports on Fishes. Reports on the results of dredging under the supervision of Alexander Agassiz, on the East coast of the United States, during the summer of 1880, by the U.S. Coast Steamer "Blake". Commander J.R. Bartlett. U.S.N. commanding. Bulletin of the Museum of Comparative Zoology,10:183-226.

_________________________. 1896. Oceanic Ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collection made by steamers "Black", "Albatross" and "Fish Hawk" in the Northwestern Atlantic. Special Bulletin of the U.S. National Museum 1985 (1986) 1 (text): 1-553; 2(atlas):1-26.

Günther, A. 1862. Catalogue of Fishes in the British Museum. Vol IV. Trustees of the British Museum. London. 534 pp.

__________. 1887. Report on the deep-sea fishes collected by H.M.S. CHALLENGER, during the years 1873-1876. Challenger Report 22 (Zoology): i-xvi + 1-335.

Haedrich, R.L. 1964. Food habits and young stages of North Atlantic Alepisaurus (Pisces, Iniomi). Brevoria 201:1-15.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana. 263 pp.

Holt, E.W.L. and L.W. Byrne. 1908. New deep-sea fishes from the south-west coast of Ireland. Annals and Magazine of Natural History, 8(1):86-95.

Howes, G.J. 1990. Biogeography of gadoid fishes. Journal of Biogeography, 18:595-622.

Hubbs, C. and K.F. Lagler. 1954. Fishes of the Great Lake region. Ann Arbor: University of Michigan Press. 213 pp.

Hureau, J. C. and Th. Monod. 1973. Check list of the fishes of the North-eastern Atlantic and the Mediterranean (Clofnan). Vol I and II. UNESCO, Paris.

Iwamoto,T. and Y.I. Sazonov. 1988. A review of the Southeastern Pacific Coryphaenoides (sensu lato) (Pisces, Gadiformes, Macrouridae). Proceedings of the California Academy of Sciences, 45(3):35-82.

Johnson, J.Y. 1862. Description of some new genera and species of fishes obtained at Madeira. Proceedings of the Scientific Meetings of the Zoological Society of London, 1862(pt 2):167-180.

____________. 1863. Description of some new genera and species of fishes obtained at Madeira. Annals and Magazine of Natural History. Series 3. vol II: 58-64.

Karrer, C. 1971. Die otolithen der Moridae (Teleostei, Gadiformes) und ihre systematische bedeutung. Zoologische Jahrbucher. Abteilung fur systematic Okologie und Geographie der Tiere, 98:153-204.

Keller, G. 1981. Planktonic foraminiferal faunas of the equatorial pacific suggest early miocene origin of present oceanic circulation. Marine Micropaleontology, 6:269-295.

Kennett, J. 1982. Marine Geology. Prentice-Hall, Inc. Englewood Cliff,. N.J. 813 pgs.

Koefoed, E. 1953. Fishes from the sea-bottom. Report on the Scientific Results of the "Michael Sars" North Atlantic Deep-Sea Expedition,1910,4 (Pt.1):1-47.

Leviton, A.E., R.H. Gibbs,Jr., E. Heal and C.E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985 (3):802-832.

Lindberg, G.V. and M.I. Legeza. 1965. Family Moridae. pp: 226-232. In: Fishes of the Sea of Japan and the adjacent areas of the Sea of Okhotsk and the Yellow Sea. Part 2. Teleostomi. 391 pag. (translated from Russian).

Lloris, D. 1986. Ictiofauna demersal y aspectos biogeográficos de la costa sudoccidental de Africa (SWA/Namibia). Monografías de Zoología Marina,1: 9-432, 228 figs.

Lowe, R.T. 1841. A synopsis of the fishes of Madeira; with the principal synonyms, Portuguese names, and characters of the new genera and species. Transactions of the Zoological Society of London, 2(3):173-200.

Lutjeharms, J. R. E. 1990. The oceanography and fish distribution of the Southern Ocean. pp. 6-27. In: O. Gon and P. C. Heemstra (eds.) Fishes of the Southern Ocean. J. L. B. Smith Inst. Ich., Grahamstown, 462 pp., 12 pls.

Maddison, W.P., M.J. Donoghue and D.R. Maddison. 1984. Outgroup analysis and Parsimony. Systematic Zoology, 33(1): 83-103.

Maddison, W.P. and D.R. Maddison. 1992. Mac Clade: Analysis of phylogeny and character evolution. Version 3.0. Sinauer Associates, Sunderland, Massachusetts.

Manugistic Inc. and Statistical Graphic Corporation. 1993. Statgraphics: statistical graphic system. User's guide. Rockville, Maryland: Statistical Graphic Corp.

Markle, D.F. 1989. Aspect of character homology and phylogeny of the gadiformes. pp.: 59-88. In: D.M. Cohen (ed.) Papers on the Systematics of Gadiforms fishes. Contribution in Science. Los Angeles County Museum of Natural History, 32:1-262.

Markle, D.F. and R. Meléndez C. 1988. A new species of *Laemonema* from off Chile, with a redescription of *L. globiceps* Gilchrist (Pisces:Moridae). Copeia 1988 (4): 871-876.

Matallanas, J. 1985. First record of the North Atlantic morid fish, *Laemonema latifrons* Holt and Byrne,1908, in the Mediterranean. Journal of Fish Biology, 26:289-290.

Matsubara, K. 1938. Studies on the Deep-Sea Fishes of Japan. IX Description of a new Gadid Fish. Bulletin of the Japanese Society of Scientific Fisheries, 7(2):61-62.

Mayden, R.L. 1988. Systematics of the *Notropis zonatus* species group, with description of a new species from the interior highlands of North America. Copeia 1988(1):153-173.

Mayden, R.L., W.J. Rainboth and D.G. Buth. 1991. Phylogenetic systematics of the cyprinid genera *Mylopharodon* and *Ptychocheilus*: Comparative morphometry. Copeia 1991(3):819-834.

McEachran, J.D. and T. Miyake. 1988. A new species of skate from the gulf of California (Chondrichthyes, Rajoidei). Copeia 1988(4):877-886.

Miller, R.G. 1993. A history and atlas of the fishes of the Antarctic Ocean. Foresta Institute for Ocean and Mountain Studies, Carson City, Nevada. 792 pags.

Nakamura, I. 1986. Salilota sp. pp: 106-107. In: Important fishes trawled off Patagonia. I. Nakamura (ed.). Japan Marine Fishery Resource Research Center, Tokyo, Japan.

Nakaya, K., K. Amaoka and K. Abe. 1980. A review of the genus Lepidion (Gadiformes, Moridae) from the Northwestern Pacific. Japanese Journal of Ichthyology, 27(1):41-47.

Nelson, G. J. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. Systematic Zoology, 27:324-345.

Nolf, D. and E. Steurbaut. 1989. Importance and restriction of the otoliths-based fossil record of gadiforms and ophidiiforms fishes. pp.: 47-58. In: D.M. Cohen (ed.) Papers on the Systematics of Gadiforms fishes. Contribution in Science. Los Angeles County Museum of Natural History, 32:1-262.

Norman, J.R. 1966. A draft synopsis of the orders, families and genera of recent fishes and fishlike vertebrates. Unpublished photo offset copies distributed by British Museum of Natural History. 649 pp.

Okamura, O. 1982. Laemonema filodorsale Okamura, Laemonema palauense Okamura. pp: 132-139. In: Fishes of the Kyushu-Palau Ridge and Tosa Bay. O. Okamura, K. Amaoka, and F. Mitani (eds.). Japan Fisheries Resource Conservation Assoc., Tokyo.

_________. 1986. Gadiformes: Moridae. pp:91-92. In: The Fishes of the Japanese Archipelago. H. Masuda, K. Amaoka, C. Araga, T. Uyeno and T. Yoshino (eds.). Tokai University Press. Japan. Text, 1-437.

Okiyama, M. 1986. Laemonema nana Taki. pp:321-323. In: An Atlas of the Early Stage Fishes in Japan. M. Okiyama (ed.).Tokai University Press,39,10 (4).

Parin, N.V. 1984. Three new species of the genus Physiculus and other fishes (Moridae, Gadiformes) from the submarine seamounts of the southeastern Pacific Ocean. Journal of Ichthyology, 24:46-60.

Parin, N.V. and Y.I. Sazonov. 1990. A new species of the genus Laemonema (Moridae,Gadiformes) from the tropical southeastern Pacific. Japanese Journal of Ichthyology, 37(1):6-9.

Patterson, C. and D.E. Rosen. 1989. The Paracanthopterygii Revisited: Order and Disorder. pp.: 5-36. In: D.M.Cohen (ed.) Papers on the Systematics of Gadiforms fishes. Contribution in Science. Los Angeles County Museum of Natural History, 32:1-262.

Paulin, C.D. 1983. A revision of the family Moridae (Pisces: Anacanthini) within the New Zealand Region. Records of the National Museum of New Zealand,2(9):81-126.

__________. 1985. A new genus and species of deepwater codfish (Pisces:Moridae) from New Zealand. New Zealand Journal of Zoology,12:357-361.

__________. 1988. Swimbladder structure in morid cods (Pisces: Gadiformes). Copeia 1988(2):450-454.

__________. 1989. Moridae: Overview. pp: 243-250 In: D.M.Cohen (ed.) Papers on the Systematics of Gadiforms fishes. Contribution in Science. Los Angeles County Museum of Natural History, 32:1-262.

Pautov, G. P. 1980. Distribution and biology of *Laemonema longipes* Shmidt, 1938. pp: 157-162. In: V. P. Shuntov (ed.) Biological resources of the Kuroshio and adjacent waters. TINRO, vol. 104, Vladivostok, U.S.S.R.

Pavlov, Yu.P. and D.P. Andrianov. 1986. A preliminary list of fishes of the Mill Submarine Elevation. Journal of Ichthyology, 26(4): 153-161.

Poll, M. 1953. Poissons III. Teleosteens malacopterigiens. Res. Sci. Exped. Oceanogr. Belge eaux cotiers Africaines de l'Atalntique Sud. (1948-1949), 4 (2):1-258.

Potthoff, T. 1984. Clearing and Staining Techniques. pp: 35-37. In: H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall,Jr. and S.L. Richardson (eds.), Ontogeny and Systematics of Fishes, Special Publication Number 1, American Society of Ichthyologist and Herpetologist, 760 pp.

Powles, H. and D.F. Markle. 1984. Identification of larvae. pp: 31-33. In: H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall,Jr. and S.L. Richardson (eds.), Ontogeny and Systematics of Fishes, Special Publication Number 1, American Society of Ichthyologist and Herpetologist, 760 pp.

Rass, T.S. 1954. Contribution to the study of Pacific Ocean Moridae (Pisces, Gadiformes). Akademiya Nauk SSSr, Trudy Instituta Okeanologii, Moscow, 9:56-61. (English translation from Russian by The Israel Program for Scientific Translation).

Shmidt, P.Yu. 1950. Fishes of the Sea of Okhotsk. Academy of Sciences of the U.S.S.R., Transactions of the Pacific Committee, 6:44-45, Plate 2.

Small, G.J. 1981. A review of the bathyal genus Antimora (Moridae: Gadiformes). Proceedings of the California Academy of Sciences,42(13):341-348.

Svetovidov, A.N. 1948. Gadiformes. In: Fauna of the U.S.S.R.. Fishes. A.A. Shtakelberg ed. Zoological Institute of the Academy of Sciences of the U.S.S.R.., Series 34, vol 9:1-103 (English translation from Russian by The Israel Program for Scientific Translation, Jerusalem).

Swofford, D.L. 1991. PAUP: Phylogenetic analysis using parsimony. Version 3.0. Computer program distributed by the Illinois Natural History Survey, Champaing, Illinois.

Taki, I. 1953. On two new species of fishes from the Inland Sea of Japan. J. Sci. Hiroshima Univ., ser. B, div. 1 (Zool.), 14:201-210.

Templeman, W. 1970. A review of the morid fish genus Lepidion of the North Atlantic with first records of Lepidion eques from the Western North Atlantic. Journal Fisheries Research Board of Canada, 27(3):457-498.

Thompson, W.F. 1916. Fishes collected by the United States bureau of fisheries steamer "Albatross" during 1888, between Montevideo, Uruguay and Tomé, Chile, on the voyage through the Strait of Magellan. Proceedings of the United States National Museum, 50:401-476.

Trunov, I.A. 1989. Fishes of the family Moridae from the Southeastern Atlantic (Genera Laemonema and Momonatira). Journal of Ichthyology,29 (2): 179-185.

__________. 1990. Fishes of the family Moridae from the Southeast Atlantic (Paralaemonema gen. et spp.n.). Voprosy ikhtiologii, 30(2):192-200.

Vaillant, L.L. 1888. Expéditions scientifiques du "Travailleur" et du "Talisman" pendant les années 1880, 1881, 1882, 1883. Poissons. Paris. 1-406.

Walker Jr.,H.J. and R.H. Rosenblatt. 1988. Pacific toadfishes of the genus Porichthys (Batrachoididae) with descriptions of three new species. Copeia 1988(4):887-904.

Watrous,J.F. and Q.D. Wheeler. 1981. The out-group comparison method of character analysis. Syst. Zool. 30(1):1-11.

Weitzman, S.H. 1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families. Bulletin American Museum of Natural History, 153:327-478.

Whitley, G.P. 1965. Some fish genera scrutinized. Proceedings of the Royal Zoological Society of New South Wales, 1964-1965: 25-26.

Wiley, E.O. 1981. Phylogenetics. The Theory and Practice of Phylogenetics Systematics. John Wiley and Sons. USA. 439 pp.

Yabe, M.; D.M. Cohen; K. Wakabayashi and T. Iwamoto. 1981. Fishes new to the eastern Bearing Sea. Fisheries Bulletin, 79(2):353-356.

APPENDIX

Appendix 1.- Abbreviations used in the figures 4 - 16.

- actinosts (A)
- arm of the hyomandibular that articulated with the opercle (AR)
- basipterygia (B)
- coracoid (C)
- cartilaginous joint (CJ)
- cleithrum (CL)
- anterior chamber (C1)
- posterior chamber (C2)
- epurals (E)
- elongate neck (EN)
- epibranchial 1 to 4 (E1 - 4)
- epibranchial 2 to 4 (E2 - 4)
- epibranchial 3 to 4 (E3 - 4)
- foramen (F)
- first rays of the first dorsal fin (F1)
- hypurals (H)
- interarcual cartilage (IC)
- interarcual ligament (IL)
- ligament (L)
- antero-lateral blade of hyomandibular (LPB)
- lower left blade of the hyomandibular (LLB)
- lower articulation in pharyngobranchial 2 (LP2)
- laminae in first pterygiophore of first dorsal fin (L1)
- maxillary (MX)
- maxillary process (MP)
- neural spines (NS)
- parahypophysis (PR)
- parahypurals (PA)
- postcleithrum (PC)
- pharyngobranchial 1 to 4 (PH1 - 4)
- ribs (R)
- scapula (S)
- strut 1 (S1)
- strut 2 (S2)
- strut 3 and 4 (S3 - S4)
- uncinate process (UP)
- total length of the hyomandibular arm (TLA)
- total length of the hyomandibular body (TLB)
- supero-posterior blade of the hyomandibular (URB)
- upper articulation in pharyngobranchial 2 (UP2)
- X bone (X)
- Y bone(Y)